Vol. 19, No. 2 November 1950

THE JOURNAL OF ANIMAL ECOLOGY

COMMONWEALTH BUREAU OF ENTOMOLOGY LIBRARY
9 Eu.431
PARATE

EDITED FOR THE

BRITISH ECOLOGICAL SOCIETY

by

CHARLES ELTON

and

DENNIS CHITTY

CAMBRIDGE UNIVERSITY PRESS
LONDON: BENTLEY HOUSE, N.W.1
NEW YORK: 51 MADISON AVENUE

Annual subscription: thirty-five shillings (twenty-five shillings to members of the British Ecological Society)

Single numbers: twenty-two shillings and sixpence

World-List abbreviation: J. Anim. Ecol.

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 19, No. 2 November 1950

CONTENTS

PAGE

Thomas Park and Marian Burton Frank. The population history of *Tribolium* free of sporozoan infection 95

T. B. Reynoldson. Natural population fluctuations of *Urceolaria mitra* (Protozoa, Peritricha) epizoic on flatworms 106

M. V. Brian. The stable winter population structure in species of *Myrmica* 119

T. T. Macan. Ecology of fresh-water Mollusca in the English Lake District 124

Winifred E. Frost. The growth and food of young salmon (*Salmo salar*) and trout (*S. trutta*) in the River Forss, Caithness . . 147

J. R. Erichsen Jones. A further ecological study of the River Rheidol: the food of the common insects of the main-stream . . . 159

H. Barnes and H. T. Powell. The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides*, after a heavy initial settlement . 175

Helen Chitty. Canadian Arctic Wild Life Enquiry, 1943–49: with a summary of results since 1933 180

Review 194

Notices of publications on the Animal Ecology of the British Isles . 195

British Ecological Society 204

THE POPULATION HISTORY OF *TRIBOLIUM* FREE OF SPOROZOAN INFECTION*

BY THOMAS PARK AND MARIAN BURTON FRANK
Hull Zoological Laboratory, The University of Chicago

(With 3 Figures in the Text)

1. INTRODUCTION

An earlier study (Park, 1948), devoted to an experimental analysis of competition between two species of flour beetles (*Tribolium confusum* Duval and *T. castaneum* Herbst), led to the following major conclusions:

(1) As single species populations ('controls') both *T. confusum* and *T. castaneum* maintained themselves successfully for essentially a 4-year period under the prevailing conditions of husbandry.

(2) There were notable differences of species rank between the census curves of the control cultures. In other words, although both *Tribolium* were successful, the population growth-form of *T. confusum* differed significantly in pattern and mean density from that of *T. castaneum*.

(3) When the two species were cultured together ('experimentals'), i.e. when a state of interspecies competition existed, one species invariably became extinct in response to this pressure of competition and the other species persisted. Of 74 replicates, *T. confusum* became extinct in 8 instances and *T. castaneum* in 66.

(4) Knowing that both species of beetles were infected with a sporozoan parasite *Adelina tribolii*, and, wishing to evaluate the relation of such infection to their population behaviour, a series of cultures, both control and experimental, was established in which the parasite had been eliminated by manipulative means. The principal findings were these:

(*a*) Non-parasitized populations of *T. confusum* behaved like parasitized populations in terms of density and pattern of growth, the only difference noted being that the former contained about 20% more imagoes (and 20% fewer larvae and pupae) than did the latter.

(*b*) Non-parasitized populations of *T. castaneum*, on the other hand, were strikingly influenced by the absence of *Adelina* infection. Their mean density, assayed over a continuous period of 1140 days, was 33·5 individuals per g. of medium to be compared with a density of 13·3 when the sporozoan was present. In short, without changing food supply or otherwise modifying experimental conditions, the equilibrium density increased some 2·5 times! There were also decided alterations in pattern of growth as well as a relative increase in the adult component of the cultures of the order, again, of 20%.

(*c*) In parasite-free competition cultures the trend in favour of *T. confusum* is reversed. *T. castaneum* persists in about two-thirds of the cases instead of in about one-tenth—a finding to be expected on the grounds that it is this species which is so markedly affected by the infection that builds up when *Adelina* is present.

A point of departure for the present paper is afforded by the above summary; especially point four. Since it is evident that *Adelina* infection is common in the genus *Tribolium*; that such infection can influence the populations of these beetles, and, that this effect is differential in the sense that it is greater for one species than for the other, it appears that additional information about the ecology of host and parasite is worthwhile both from technical and theoretical viewpoints.

The census history of control, unparasitized cultures of *T. confusum* and *T. castaneum* was followed for 1140 days in the initial study. As these data were being analysed for publication it was decided that, owing to their inherent interest, the cultures should not be discontinued but, rather, maintained for a still greater time with the eventual aim of reporting upon them in more detail than was feasible earlier. The populations now have an unbroken history of 2070 days, or nearly 6 years. This encompasses approximately 69 *Tribolium* generations. They have been carried on in some replication. The technique of census allows a complete and accurate enumeration of numbers and is not based on sampling. The nutritive and environmental conditions are

* The authors wish to express their sincere appreciation to Mr P. H. Leslie, Bureau of Animal Population, Oxford, for his critical reading of the manuscript and for helpful suggestions. This investigation was supported by a grant from the Doctor Wallace C., and Clara A. Abbott Memorial Fund of the University of Chicago.

standardized and have been controlled with what appears to be negligible error.

2. METHODS

Although a detailed discussion of methods is to be found in Park (1948), a few comments are appropriate here.

Medium and environmental control. The experimental work conducted with *Tribolium* in this laboratory makes use of a 'standard medium' consisting of 95 % whole-wheat flour and 5 % brewer's yeast powder. The flour and yeast are pre-sifted through a no. 8 bolting cloth sieve to obtain particles smaller in size than any of the living stages. After such treatment the two components are thoroughly mixed together by mechanical means in order to ensure homogeneous distribution. The populations discussed in this paper are maintained in shell vials containing 8 g. of medium.

All cultures are kept in dark incubators at a constant temperature of 29·5° C. (±0·5°), and a relative humidity characteristically ranging from 60 to 75 %. The conditions occasionally deviate beyond these limits; a point meriting later discussion.

Census procedure. Every culture is counted each 30 days. The medium is screened through silk bolting cloth of selected meshes which facilitates separation and recovery of all stages. At the time of census the numbers of larvae, pupae, and imagoes are counted and recorded; the eggs are collected and saved but not counted, and the entire living population, free of frass and other debris, is returned to 8 g. of fresh medium for another 30-day period.

Parasitization. Although a considerable literature now exists about the genus *Adelina* it does not seem relevant to review it here. If interested, the reader will find a general account in Steinhaus (1949); the original description of *A. tribolii* in Bhatia (1937); the technique by which the beetles' eggs can be freed of the infection in Park & Burrows (1942); and a discussion of the life cycle in Park (1948). Despite this literature, however, it would be misleading to suggest that the *Tribolium-Adelina* nexus is well understood. Many aspects dealing with epidemiology, pathogenicity, the possible development of host immunity, and details of transmission remain to be explored. These are avenues for future research. They cannot be discussed here. For present purposes three points need to be established. (1) The beetles acquire the infection either by taking medium containing the infective stages (oocysts) into their gut, or by cannibalizing parasitized beetles, or, through both means. (2) When the hosts become infected to a sufficient degree (whatever that may be), mortality, especially of late larval instars and pupae, results. This mortality, as we have remarked, appears to be greater for *Tribolium castaneum* than for *T. confusum*. (3) By washing the eggs in soap solution the oocysts that adhere to the sticky egg membrane are removed. If the first instar larvae developing from these treated eggs are reared in clean medium, and, if suitable precautions against subsequent infection are ensured, populations usually can be maintained in a non-parasitized condition.

In this paper we analyse the census history of populations of *T. confusum* and *T. castaneum* reared apart as control cultures and unencumbered by parasitic disease. All the conditions of experiment are identical for both species and conform to the specifications set forth above. When the populations were started on the first day, each vial, containing 8 g. of fresh medium, received four young male and four young female imagoes. On day 30 the first count was made, the counts being continued thereafter until 68 additional censuses had been taken. As is apparent from the two right-hand columns of Table 1, the number of replicates is reduced with time because certain cultures inadvertently became infected and had to be dropped from the computations (see discussion of this point in Park, 1948). The earlier study covered 1140 days. The present paper extends the data from day 1170 to day 2070 and pays greater attention to such matters as variability and the performance of individual, as contrasted to average, populations. In assembling these data, five cultures were added to the *T. confusum* component at day 1170 bringing the total up to 20, and three were added to the *T. castaneum* component increasing the total to 12. Much earlier, these 'extra' cultures had been unparasitized experimental populations in which one or the other beetle became extinct through competitive processes (see point (4*c*) in the summary on the first page of this article). The addition of eight replicates increases the scope of the study and seems to be completely legitimate. It has been abundantly shown that both species of beetles, statistically speaking, behave exactly like their always-control counterparts some time after the disappearance of their former cohabitant.

3. ANALYSIS OF DATA

This paper is organized according to the following plan. First, the data describing the census-by-census behaviour of grouped replicates for the two species are briefly presented (Table 1 and Fig. 1). Secondly, the period of observation taken as a whole is considered; census age is eliminated by averaging all comparable replicates and the emphasis is placed on the *level* of performance rather than on temporal deviations between counts (Tables 2 and 3; Fig. 2). This treatment involves mean density as well as percentage composition and some comparisons are made

with the parasitized cultures described in the earlier study. Thirdly, the matter of variability is discussed.

The census data. The anatomy of Table 1, which may be properly viewed as the 'master table' of the entire study, deserves comment. The first column sets forth census age reported at 30-day intervals. The initial census was taken on day 30, the last on day 2070. The next six columns contain figures on population density expressed as mean number per gram of medium. These figures were got by summing the total numbers for each appropriate age and species; dividing by the number of replicates to obtain the mean number per vial, and then dividing by 8 (since being three curves depicting, respectively, total population, imago population and immature population. The middle graph is similar in presentation except that it deals with *T. confusum*. The bottom graph reports total density only. It has four components: *T. castaneum*, parasitized and unparasitized; *T. confusum*, parasitized and unparasitized. Data for the parasitized cultures were taken directly from the paper of Park (1948, tables 2 and 5).

An obvious but crucial point, immediately made by Table 1, relates to the fact that all populations of both species were successful in the sense that extinctions did not occur and that there were no pro-

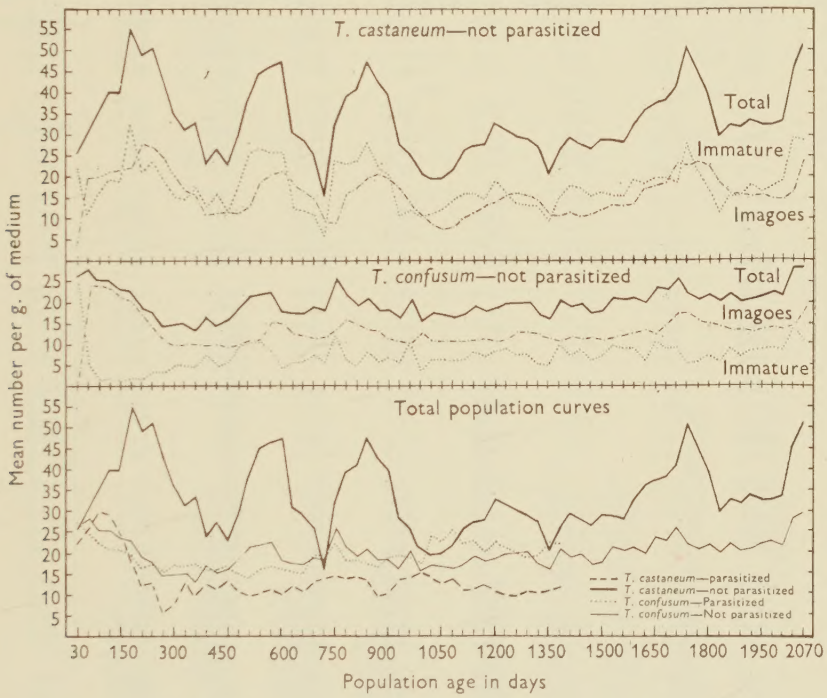


Fig. 1. Census curves for *Tribolium confusum* and *T. castaneum*: mean density plotted against time.

there are 8 g. of medium per container) to convert to number per gram. Columns 2 and 3 report density of larvae + pupae for both species; columns 4 and 5, imago density; and columns 6 and 7, total population. The next four columns (8–11) deal with percentage composition or the ratio of immature to mature stages. The last two columns (12 and 13) list the number of populations of *T. confusum* and *T. castaneum* under observation at each census. We have already discussed the reasons for the drop in these figures up to day 1170 and their increase thereafter.

Fig. 1 graphs the density data of Table 1. The top graph shows the performance of *T. castaneum*; there longed, irreversible declines in density. Thus, it can be taken as fact that the conditions of maintenance and handling impose no restriction on the cultures, even over such a long span of time. The findings suggest also that, despite the degree of inbreeding that must obtain, deleterious genetic changes do not accumulate or become intensified in these populations as they pass through 69 generations.

Table 1 indicates that the two species, while displaying a pattern characteristic for each, differ markedly one from the other. Such differences are more appropriately dealt with later. Suffice it to say here that even cursory inspection of the columns

Table 1. *Population density and percentage composition of replicated cultures of unparasitized* Tribolium confusum *and* T. castaneum *censused at 30-day intervals for 2070 days*

Census age (days)	Mean no. per gram of medium: Larvae + pupae		Imagoes		Total		Percentage: Larvae + pupae		Imagoes		No. of replicates	
	T. con.	*T. cas.*	*T. con.*	*T. cas.*	*T. con.*	*T. cas.*	*T. con.*	*T. cas.*	*T. con.*	*T. cas.*	*T. con.*	*T. cas.*
30	25·0	22·2	1·1	3·4	26·1	25·6	95·6	86·8	4·4	13·2	20	20
60	5·0	10·9	23·2	19·3	28·2	30·2	17·8	36·1	82·2	63·9	20	20
90	1·5	15·6	23·6	19·6	25·1	35·2	6·1	44·3	93·9	55·7	20	20
120	2·1	18·7	22·9	21·1	25·0	39·8	8·3	47·1	91·7	52·9	20	20
150	1·2	18·0	21·7	21·8	22·9	39·8	5·1	45·2	94·9	54·8	20	20
180	2·2	32·0	20·0	22·3	22·2	54·3	10·0	58·9	90·0	41·1	20	19
210	2·0	20·8	16·7	27·7	18·7	48·5	10·6	42·8	89·4	57·2	20	18
240	3·6	23·5	13·8	26·8	17·4	50·3	20·9	46·8	79·1	53·2	20	18
270	3·2	18·6	10·8	24·3	14·0	42·9	22·9	43·4	77·1	56·6	20	18
300	4·9	15·1	9·4	20·0	14·3	35·1	34·3	43·1	65·7	56·9	20	18
330	4·8	14·7	9·6	16·9	14·4	31·6	33·3	46·6	66·7	53·4	20	18
360	4·2	17·0	9·6	15·6	13·8	32·6	30·4	52·2	69·6	47·8	20	18
390	7·2	12·5	9·7	10·8	16·9	23·3	42·5	53·6	57·5	46·4	17	18
420	4·3	15·4	9·9	11·3	14·2	26·7	30·6	57·6	69·4	42·4	17	18
450	5·4	11·2	9·5	11·5	14·9	22·7	36·6	49·3	63·4	50·7	17	18
480	8·4	17·6	9·5	11·4	17·9	29·0	47·1	60·6	52·9	39·4	17	18
510	10·8	25·3	10 5	12·6	21·3	37·9	50·4	66·9	49·6	33·1	17	18
540	10·7	26·3	11·0	18·1	21·7	44·4	49·5	59·2	50·5	40·8	17	18
570	7·8	25·8	14·5	20·6	22·3	46·4	34·8	55·7	65·2	44·3	17	18
600	3·7	25·9	14·0	21·3	17·7	47·2	20·9	54·8	79·1	45·2	17	18
630	5·4	12·2	12·0	17·9	17·4	30·1	30·8	40·5	69·2	59·5	17	17
660	5·8	11·9	11·5	16·5	17·3	28·4	33·2	42·1	66·8	57·9	16	17
690	7·2	10·6	11·0	14·7	18·2	25·3	39·6	41·9	60·4	58·1	16	17
720	5·7	6·0	12·0	9·4	17·7	15·4	32·4	39·1	67·6	60·9	16	17
750	12·0	23·2	13·3	8·9	25·3	32·1	47·2	72·2	52·8	27·8	16	17
780	6·2	22·9	15·6	15·3	21·8	38·2	28·6	60·1	71·4	39·9	16	17
810	4·4	23·3	14·6	17·2	19·0	40·5	23·2	57·5	76·8	42·5	16	17
840	7·5	27·6	13·3	19·6	20·8	47·2	36·0	58·4	64·0	41·6	16	16
870	5·3	22·4	12·6	20·1	17·9	42·5	29·3	52·8	70·7	47·2	16	14
900	6·7	20·2	11·1	19·6	17·8	39·8	37·7	50·8	62·3	49·2	16	13
930	5·6	10·9	10·5	17·0	16·1	27·9	34·6	39·1	65·4	60·9	15	13
960	10·2	11·9	10·1	13·7	20·3	25·6	50·2	46·5	49·8	53·5	15	11
990	3·5	10·5	12·4	10·6	15·9	21·1	21·9	49·5	78·1	50·5	15	11
1020	6·1	10·9	10·6	8·6	16·7	19·5	36·9	56·0	63·1	44·0	15	10
1050	6·2	12·3	10·5	7·5	16·7	19·8	37·0	62·0	63·0	38·0	15	9
1080	6·0	14·3	10·5	7·6	16·5	21·9	36·5	65·4	63·5	34·6	15	9
1110	6·2	15·8	10·5	10·1	16·7	25·9	37·2	61·1	62·8	38·9	15	9
1140	7·9	15·8	10·7	11·6	18·6	27·4	42·6	57·5	57·4	42·5	15	9
1170	6·8	14·6	10·9	13·1	17·7	27·7	38·4	52·7	61·6	47·3	20	12
1200	7·8	18·5	10·3	14·0	18·1	32·5	43·1	56·9	56·9	43·1	20	12
1230	8·2	16·0	11·3	15·6	19·5	31·6	42·1	50·6	57·9	49·4	20	12
1260	7·1	13·8	12·5	16·0	19·6	29·8	36·2	46·3	63·8	53·7	20	12
1290	6·3	13·4	12·3	15·5	18·8	28·9	33·5	46·4	66·5	53·6	20	12
1320	5·0	12·7	12·2	14·3	17·2	27·0	29·1	47·0	70·9	53·0	20	12
1350	4·8	9·3	11·2	11·3	16·0	20·6	30·0	45·2	70·0	54·8	20	12
1380	9·8	15·0	10·6	10·9	20·4	25·9	48·0	57·9	52·0	42·1	20	12
1410	7·0	17·6	11·7	11·6	18·7	29·2	37·4	60·3	62·6	39·7	20	12
1440	8·5	17·1	10·8	10·6	19·3	27·7	44·0	61·7	56·0	38·3	20	12
1470	6·1	15·1	11·2	11·2	17·3	26·3	35·3	57·4	64·7	42·6	20	12
1500	7·1	16·4	10·6	12·1	17·7	28·5	40·1	57·5	59·9	42·5	20	12
1530	9·6	15·3	11·3	13·3	20·9	28·6	45·9	53·5	54·1	46·5	20	12
1560	8·5	15·1	12·3	13·2	20·8	28·3	40·9	53·4	59·1	46·6	20	12
1590	8·5	19·2	12·5	13·4	21·0	32·6	40·5	58·9	59·5	41·1	20	12
1620	6·4	18·5	13·5	17·0	19·9	35·5	32·2	52·1	67·8	47·9	20	12
1650	10·6	19·4	12·4	17·8	23·0	37·2	46·1	52·2	53·9	47·8	20	12
1680	8·4	19·6	14·4	18·5	22·8	38·1	36·8	51·4	63·2	48·6	20	12
1710	8·5	18·6	17·3	22·6	25·8	41·2	33·0	45·2	67·0	54·8	20	12
1740	5·0	27·7	17·3	22·5	22·3	50·2	22·4	55·2	77·6	44·8	20	12
1770	5·2	21·7	15·7	23·2	20·9	44·9	24·9	48·3	75·1	51·7	20	12
1800	7·3	16·9	14·9	22·4	22·2	39·3	32·9	43·0	67·1	57·0	20	12
1830	5·9	11·7	14·5	18·2	20·4	29·9	28·9	39·1	71·1	60·9	20	12
1860	8·8	16·0	13·4	16·4	22·2	32·4	39·6	49·4	60·4	50·6	20	12
1890	7·2	15·9	13·5	16·2	20·7	32·1	34·8	49·5	65·2	50·5	20	12
1920	8·1	17·9	13·2	15·3	21·3	33·2	38·0	53·9	62·0	46·1	20	12
1950	8·2	16·7	13·9	15·8	22·1	32·5	37·1	51·4	62·9	48·6	20	12
1980	8·8	17·7	14·0	14·8	22·8	32·5	38·6	54·5	61·4	45·5	20	12
2010	8·4	18·9	13·8	14·8	22·2	33·7	37·8	56·1	62·2	43·9	20	12
2040	14·1	29·2	14·8	16·7	28·9	45·9	48·8	63·2	51·2	36·8	20	12
2070	11·1	28·4	18·0	23·4	29·1	51·8	38·2	54·8	61·8	45·2	20	12

immediately shows that *T. castaneum* consistently persists at greater densities (immature, imago, and total) than does *T. confusum*; that the latter species is noted for a higher percentage of imagoes, and a lower percentage of larvae + pupae, than the former, and that *T. castaneum* is subject to fluctuations in total density considerably greater in magnitude than those of its relative. The last point is well documented in Fig. 1 and may be elaborated as follows.

the percentage composition of immature relative to mature components; and in Table 4 which compares total population density for the entire term of observation with certain census intervals strategically selected from that term. In order to assess the effect of parasitization on these various 'equilibria', Table 4 includes information as to what happens when the cultures are known to be diseased, see also Fig. 2.

Turning attention to Table 2 it can be seen that

Table 2. *Mean density of unparasitized* Tribolium confusum *and* T. castaneum *populations for the total period of observation (expressed as number of individuals per gram of medium)*

Species	Categories	Range		Mean	Days observed
		Maximum	Minimum		
T. confusum	Larvae + pupa	14·1	1·2	6·69	2070
	Imagoes	23·6	9·4	13·08	2070
	Total	29·1	13·8	19·77	2070
T. castaneum	Larvae + pupae	32·0	10·5	17·53	2070
	Imagoes	27·7	7·5	16·03	2070
	Total	54·3	15·4	33·56	2070

Fig. 2. Performance of *T. confusum* and *T. castaneum* expressed in terms of density and percentage composition for the total period of observation. Bars are, respectively from left to right, immatures, adults, and totals.

Treatment by grouped census intervals. A clear understanding of the general differences in performance between *T. confusum* and *T. castaneum*, as well as the effect that *Adelina* exerts on populations of both species, emerges when the period as a whole is examined, ignoring all census-to-census variations. The data requisite for such an examination appear in three tables: in Table 2 which tabulates density as number per gram of medium; in Table 3 which lists

T. castaneum, when uninfected, maintains much greater average densities than does *T. confusum*. For the entire period (excluding only the atypical day 30 census because at that time the populations are largely composed of first generation immatures) *T. castaneum* persists at 33·56 individuals per gram of medium and *T. confusum* at 19·77. We are not aware of any reliable, and readily applied, method for estimating the significance of the difference between

these two means. The usual method of mean difference ± standard error is inappropriate because the censuses reported in Table 1 are not independent observations. However, it is permissible to compute the standard errors of the means for any one census age and then compare the two species as of that time. This has been done for selected population ages in Table 5 where the right-hand column reports the difference: *T. castaneum* minus *T. confusum* ± S.E. Of these eleven comparisons, nine are significant (at $P < 1\%$); one, the day 1020 record, is not significant, and the day 720 comparison is invalid as explained on p. 101, footnote. Thus it seems clear, as indeed common sense dictates, that there is no reasonable doubt that the two means reflect real biological differences rather than errors of random sampling.

The figures listed in Table 2 under 'range' afford some measure of the span of variation in density. These ranges are selected from the census data reported in Table 1 and, as such, they are averages and not the maximum and minimum numbers found in individual populations. In some respects the latter are more entertaining for they show how large, and how small, populations under our conditions of experiment *can* become without adversely affecting their later history. The following array is offered in illustration:

(Maximum) − (Minimum) (Difference)

T. confusum

51·4 (at day 2070) − 7·6 (at day 420) = 43·8

T. castaneum

97·7 (at day 570) − 11·7 (at day 1020) = 86·0

It is at once apparent that the ranges for individual populations are considerably in excess of those based on grouped data—a fact especially evident for the maximum readings. The difference between extremes is two times greater for *T. castaneum* than for *T. confusum* which substantiates conclusions that have already been advanced. It is noteworthy that populations of *T. castaneum* do attain total densities of nearly 100 individuals per gram of flour. This was quite unanticipated in earlier days when parasitized stocks were used almost exclusively.*

There is good reason for examining the total period of census from the viewpoint of percentage composition as well as density for this leads to some indications regarding age-distribution. The reason becomes more compelling when it can be shown that the two species maintain their populations with different ratios of mature to immature stages. This was originally reported by Park (1948) and receives further substantiation in the present study. In sum, *T. castaneum*, irrespective of the fact that the *totals* of both larvae, pupae, and imagoes are higher, consistently persists with some 20% greater number of immature, and a 20% smaller number of mature, individuals than does *T. confusum*. The actual mean differences taken from Table 3 are

Larvae + pupae

(*T. castaneum* − *T. confusum*) 52·1 − 33·9 = 18·2%

Imagoes

(*T. confusum* − *T. castaneum*) 66·1 − 47·9 = 18·2%

It is significant that the species differences just described exist for the entire tenure of the experiment. This can be seen from columns 8 and 9 of Table 1 from which it is evident that there is only one departure from the trend. Excluding the day 30 records for reasons already discussed, the single instance in which the percentage of immature stages of *T. castaneum* falls below *T. confusum* occurs at day 960. When the percentage of larvae + pupae is plotted against time the resulting curve describing *T. confusum* drops to a low level in the early days of growth (day 90 to day 210); rises steadily until day 300, and then fluctuates about its mean value of 34%. The curve for *T. castaneum* is essentially similar apart from the fact, of course, that its position with reference to the ordinate is some 20% higher. The single discrepancy is that the curve for this species approaches its mean much earlier, well before day 300. It is reasonable to infer from these data that, after roughly a year's time, the age-distribution for both species is approximately stabilized.

Table 4 allows a comparison to be made of selected intervals, as well as facilitating an analysis of the

Table 3. *Percentage composition of unparasitized* Tribolium confusum *and* T. castaneum *populations for the total period of observation of* 2070 *days* (*expressed as mean percentage larvae + pupae and imagoes*)

Species	Categories	Range		Mean
		Maximum	Minimum	
T. confusum	Larvae + pupae	50·4	5·1	33·9
	Imagoes	94·9	49·6	66·1
T. castaneum	Larvae + pupae	72·2	36·1	52·1
	Imagoes	63·9	27·8	47·9

* In experiments now in progress in this laboratory under experimental conditions similar to those reported here, one population of unparasitized *T. castaneum* attained a total size of 1140 individuals per 8 g. of medium or a density of 142·5 per g.! This is, by far, the most crowded population we have ever, somewhat wearily, counted.

Table 4. *Mean density of parasitized and unparasitized* Tribolium confusum *and* T. castaneum *populations for selected intervals of census (expressed as total population per gram of medium)*

Census interval (days)	Species	*Adelina* (+ or −)	Range		Mean
			Maximum	Minimum	
30–2070	*T. confusum*	−	29·1	13·8	19·77
	T. castaneum	−	54·3	15·4	33·56
30–1050	*T. confusum*	−	28·2	13·8	18·88
	T. castaneum	−	54·3	15·4	34·46
1050–2070	*T. confusum*	−	29·1	16·0	20·65
	T. castaneum	−	51·8	20·6	32·67
0–1380	*T. confusum*	−	28·2	13·8	18·87
	T. castaneum	−	54·3	15·4	32·53
	*T. confusum**	+	25·6	13·6	19·25
	*T. castaneum**	+	29·3	9·1	13·30

* Data from Park (1948).

relation of parasitic disease to mean density. The first two rows of the table repeat data already discussed (Table 2). It was considered informative to divide the total period of observation into halves, each of nearly 3 years' duration, so that the average densities characteristic of the two species could be examined within this frame of reference. The requisite figures appear in the third and fourth (30–1050) and the fifth and sixth (1050–2070) rows of Table 4. When these two periods are contrasted for each species it is evident that the mean densities shift very little between the earlier and later intervals. *T. confusum* increases from 18·88 to 20·65 per g. *T. castaneum* drops from 34·46 to 32·67. From this it follows that population age does not induce any marked alteration of *mean* density when the food supply is regularly replenished, the physical environment is controlled, and 'conditioning' of the flour (see chap. 22 in Allee, Emerson, Park, Park & Schmidt, 1949) is minimized. The fact that average equilibria, characteristic for each species, persist for long periods despite the demonstrated presence of considerable census fluctuations from count to count, is of some general ecological interest.

In the bottom four rows of Table 4 there are listed the equilibrium densities for *T. confusum* and *T. castaneum*, both parasitized and unparasitized. The data are taken from Park (1948) except that additional counts have been added to the non-infected group from the new information presented in this study in order to increase the observation time of this series to 1380 days. The principal conclusions are as follows:

(1) *T. confusum* populations maintain a similar mean density irrespective of whether *Adelina* is present or absent.

(2) When infected with *Adelina*, *Tribolium castaneum* exhibits an equilibrium density some 60% below the non-infected counterpart.

(3) When both species are infected, *T. confusum* maintains larger populations than *T. castaneum*, namely: 19·25 − 13·30 = 5·95. Contrariwise, as noted earlier, when neither species is infected it is *T. castaneum* that achieves the higher densities: 32·53 − 18·87 = 13·66.

Fig. 2 shows these characteristic differences both in terms of mean number per gram of medium and percentage composition.

Variability and growth form. The interesting fact that populations of flour beetles maintain characteristic average densities for extended periods has been noted. But to complete the analysis it is relevant to say something about variability in census performance and to discuss the even more important question of the growth pattern assumed by both species when density is plotted against culture age. Variability affords insight into the homogeneity of the data. Pattern, dealing as it does with observed group behaviour, describes those features essential to any understanding of population phenomena. We examine the question of variation by computing standard deviations and coefficients of variability for selected census ages. Certain comments about individual cultures appear shortly.

It is clear from even cursory inspection of Fig. 1 that *T. castaneum* fluctuates in a somewhat oscillatory fashion. The curve describes peaks, followed by valleys, followed by peaks, and so on. In Table 5, eleven census dates have been chosen arbitrarily to compare these high and low periods. Thus, days 180, 600, 840, 1200, 1740, and 2070 are times of large populations while days 450, 720, 1020, 1350, and 1830 represent the nadirs.* For purposes of species

* Day 720 is a special case because incubator failure lowered the temperature from 29·5° C., to that of the laboratory room for several weeks preceding the census. In all probability, this exaggerated the decline already under way. The matter is discussed more fully in Park (1948, p. 279).

Table 5. *Biometric constants for unparasitized populations of* Tribolium castaneum *and* T. confusum *for selected census ages (expressed as number per gram of medium)*

Census age (days)	*T. castaneum*				*T. confusum*				*T. castaneum* minus *T. confusum* ± S.E.
	Mean ± S.E.	S.D.	C.V.	N	Mean ± S.E.	S.D.	C.V.	N	
180	54·3 ± 3·21	14·0	25·8	19	22·2 ± 0·85	3·8	17·1	20	32·1 ± 3·32*
450	22·7 ± 1·98	8·4	37·0	18	14·9 ± 0·65	2·7	18·1	17	7·8 ± 2·08*
600	47·2 ± 5·11	21·7	46·0	18	17·7 ± 0·87	3·6	20·3	17	29·5 ± 5·18*
720	15·4 ± 1·14	4·7	30·5	17	17·7 ± 0·98	3·9	22·0	16	−2·3 ± 1·50
840	47·2 ± 3·15	12·6	26·7	16	20·8 ± 1·03	4·1	19·7	16	26·4 ± 3·31*
1020	19·5 ± 1·80	5·7	29·2	10	16·7 ± 0·54	2·1	12·6	15	2·8 ± 1·88
1200	32·5 ± 2·14	7·4	22·8	12	18·1 ± 0·47	2·1	11·6	20	14·4 ± 2·19*
1350	20·6 ± 1·47	5·1	24·8	12	16·0 ± 0·58	2·6	16·3	20	4·6 ± 1·58*
1740	50·2 ± 5·46	18·9	37·6	12	22·3 ± 1·43	6·4	28·7	20	27·9 ± 5·64*
1830	29·9 ± 2·68	9·3	31·1	12	20·4 ± 0·83	3·7	18·1	20	9·5 ± 2·81*
2070	51·8 ± 5·80	20·1	38·8	12	29·1 ± 1·74	7·8	26·8	20	22·7 ± 6·06*

* Signifies significant difference at $P < 5\%$.

contrast similar statistics are included for *T. confusum*, but these do not necessarily represent extremes of density. There is no point in elaborating upon the means of Table 5 except to note that for *T. castaneum* all 'high' means are very different from all 'low' means except the comparison between the day 1200 and day 1830 censuses; 32·5 and 29·9, respectively. When the standard deviations listed for *T. castaneum* are examined it is in general true, as would be expected, that they are larger when their means are larger. The coefficients of variability, however, are more informative. There is no suggestion that they are consistently higher when the populations are large, or vice versa. In short, relative variation does not seem to be related to numbers per gram. As a matter of fact, most of these coefficients are quite similar one with the other. The new point added by the data dealing with *T. confusum* is that the coefficients of variability are consistently lower for this species than for its relative.

Our attention now turns briefly to the pattern of growth and maintenance displayed by the two species of beetles under the described conditions of experiment. The matter is dealt with both in terms of averages and the behaviour of individual cultures.

Growth form of T. castaneum. We have already alluded to the pattern displayed by *T. castaneum* but further comment is in order. From the top graph of Fig. 1 it is evident that this species departs with some regularity from a position of mean equilibrium. In fact, the concept of equilibrium is an artifact in the sense that it is not temporally sustained as such for relatively brief spans of time. On the other hand, it has real statistical validity as a description of average density levels as has already been noted. Certain points about the fluctuations are assembled in Table 6. This table lists those ages in the grouped history of the cultures at which highest, and lowest, densities occur along with the duration of the intervals when growth or decline are in progress. The length of the increase and decrease periods looks like this:

Duration of increase period (days): 180, 150, 120, 180, 390, 240
Duration of decrease period (days): 270, 120, 180, 150, 90

Depending on the point of view, there are elements of both regularity and irregularity in these data. If one excludes the interval lasting 390 days (and there is no known legitimate reason for doing so) increase and decrease intervals have some semblance of conformity. On the average, the populations drop from maxima to minima somewhat faster than they build up, but the periods are of the same general order of magnitude. But when the extended 390-day interval is included the notion of irregularity gains added emphasis. We can formulate no rational hypothesis at this time to account for this longer growth period. The essential position seems to be that *T. castaneum* does most certainly fluctuate; that the fluctuations are real phenomena, but that they cannot be referred to as 'cyclic' as that term is commonly understood in ecological literature.

There was a modest uncontrolled variation in our experimental incubator. This took the form that relative humidity tended at times to be lower than the prescribed levels during the winter months. There were also periods during the summer when the temperature increased 0·5° C. above the permitted range for a few days. But, clearly, these are not causal agents in shaping the fluctuations, despite the demonstration that *Tribolium* is known to be sensitive to such stimuli (Holdaway, 1932; Park & Frank, 1948). The third and fourth columns of Table 6 show that, during the summer months of certain years, the populations are at maximum in May, June, September and August. Contrariwise, minimum readings are seen during August and July of other years. Just as significant are the winter records. During February,

Table 6. *Selected data dealing with* Tribolium castaneum *at periods of maximum and minimum population density*

Census interval (days)	Duration of interval (days)	Date of last census in interval	Population trend in interval	Means at last census of interval: Numbers per gram: Immatures	Numbers per gram: Imagoes	Numbers per gram: Total ± S.E.	Percentage of: Immatures	Percentage of: Imagoes
0– 180	180	May 1944	Increasing	32·0	22·3	54·3 ± 3·21	58·9	41·1
180– 450	270	Feb. 1945	Decreasing	11·2	11·5	22·7 ± 1·98	49·3	50·7
450– 600	150	June 1945	Increasing	25·9	21·3	47·2 ± 5·11	54·8	45·2
600– 720	120	Oct. 1945	Decreasing	6·0	9·4	15·4 ± 1·14	39·1	60·9
720– 840	120	Feb. 1946	Increasing	27·6	19·6	47·2 ± 3·15	58·4	41·6
840–1020	180	Aug. 1946	Decreasing	10·9	8·6	19·5 ± 1·80	56·0	44·0
1020–1200	180	Feb. 1947	Increasing	18·5	14·0	32·5 ± 2·14	56·9	43·1
1200–1350	150	July 1947	Decreasing	9·3	11·3	20·6 ± 1·47	45·2	54·8
1350–1740	390	Sept. 1948	Increasing	27·7	22·5	50·2 ± 5·46	55·2	44·8
1740–1830	90	Dec. 1948	Decreasing	11·7	18·2	29·9 ± 2·68	39·1	60·9
1830–2070	240	Aug. 1949	Increasing	28·4	23·4	51·8 ± 5·80	54·8	45·2

two maxima and one minimum are to be noted, and December contributes another minimum also. So it seems a fair inference that uncontrolled 'climate' is not causal—an inference which leaves the facts to be accounted for by intraspecies density-dependence.

Table 6 suggests that maxima are likely to be associated with a high *percentage* of immature stages and minima with a low percentage, an exception being seen at day 1020. Fig. 1 shows a conformity between the curve for immatures and totals; this is especially marked at times of peak abundance. The curve for adult beetles tends to lag behind that for larvae, as might be expected, since the length of the developmental period approximates the span between censuses. Thus, there are indications of shifts in age-distribution (immature : mature) associated with growth form. But whether these are causal or resultant must await more direct study.

Because the pattern of growth of *T. castaneum* is so altered by the presence of *Adelina*, no consistent similarity between the curves of parasitized and unparasitized cultures can be detected (Fig. 1).

Growth form of Tribolium confusum. The growth form displayed by *T. confusum* in Fig. 1 is not so striking in its fluctuation pattern as that for *T. castaneum*. There are, however, certain features of similarity and dissimilarity. Although not particularly evident visually, a tendency exists for high and low densities of *T. confusum* to occur in association with those of *T. castaneum*; note the bottom graph of Fig. 1. Since both groups were maintained in the same incubator and accordingly shared a common physical environment such association might lend credence to the suggestion that the two species were responding to slight variations from the norm. The matter is dealt a formidable blow, however, when it is seen that an equally great association exists between non-infected and infected *T. confusum* cultures which had been started many months apart in different incubators. This strengthens the conclusion that *Adelina* has but minor effect on *T. confusum* in contrast to its effect on *T. castaneum*.

Several other suggestions arise from Fig. 1: (1) the imago curve for *T. confusum* (middle graph) is consistently higher with reference to the larval curve than is the case for *T. castaneum*; (2) the curve for immatures again parallels the total density curve with appreciable fidelity; (3) the imago curve is quite level after day 300; (4) the two species display different patterns during the first year of existence.

Behaviour of individual cultures. It is desirable in any study of population ecology so to design the investigation that comparable cultures are suitably replicated. By doing this, average trends can be described, variability assessed, and exceptional events noted and catalogued. It is also important to emphasize the behaviour of individual populations in order that their deviations from each other and from the mean of the array to which they belong can be appraised. As an illustration, we have chosen to deal briefly with this question by making use of the total data for *T. castaneum* covering the interval, 1170–2070 days. *T. castaneum* is allotted greater attention because of its higher relative variation and because its growth form is more exaggerated.

In Fig. 3, twelve separate graphs each appearing as a broken line depict the pattern of growth of twelve corresponding *T. castaneum* replicates. The solid line repeated in each graph is the mean curve adapted from Table 1 which describes the entire group.

Certain facts can be derived from the figure. As a rule, there is close conformity between the curves for individual cultures and their mean. Of the twelve, graphs 1, 3, 4, 5, 6, 8, 9, 11 and 12 do not depart from

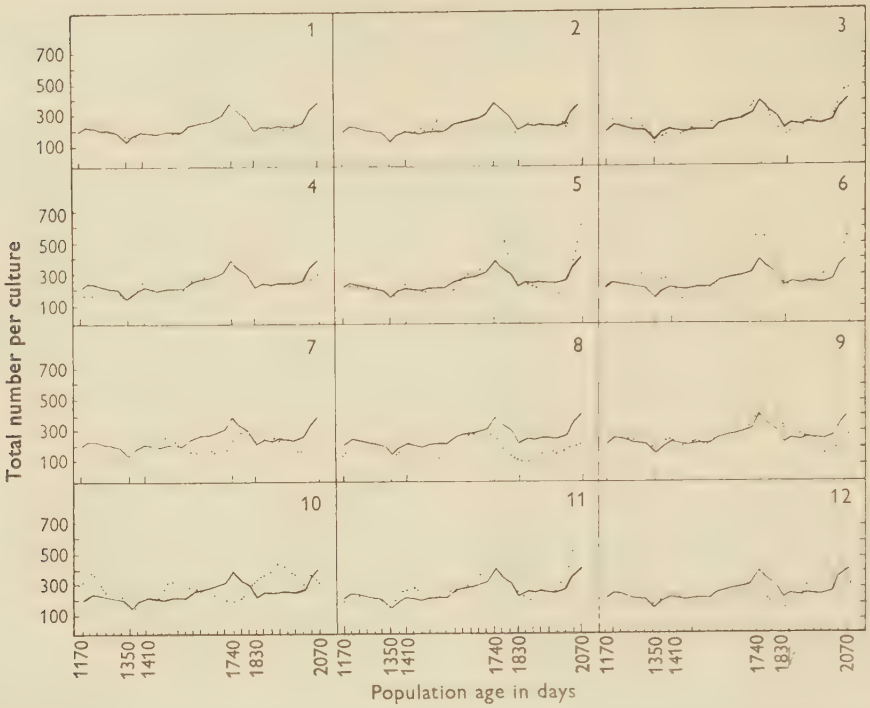


Fig. 3. Census performance of 12 individual, replicated populations over the interval 1170–2070 days (broken line) compared with the mean curve for the array over the same period of time (solid line). All cultures *T. castaneum*.

Table 7. *Density maintained by individual populations of* Tribolium castaneum *and* T. confusum *for* 31 *consecutive censuses covering the interval*: 1170–2070 *days* (*expressed as number per gram of medium*)

Population no.	Mean per vial	
	T. castaneum	*T. confusum*
1	31·0	15·0
2	29·3	19·3
3	35·6	17·8
4	35·6	19·2
5	35·7	25·2
6	39·8	17·0
7	29·6	21·7
8	23·6	22·0
9	35·2	20·0
10	37·2	24·6
11	38·9	21·5
12	29·3	25·4
13	—	23·1
14	—	23·2
15	—	23·4
16	—	22·0
17	—	19·3
18	—	19·1
19	—	20·8
20	—	19·1
Mean	33·4	20·9

average more than would be expected for biological data of this sort and perhaps less so. Naturally, there are individual discrepancies. But it seems clear that the mean is a fair representation of the *pattern*. Graph 2 shows considerable irregularity around day 1740 in that it fails to display the peak characteristic of that census. It is, however, quite confluent during earlier, and later, stages. Graphs 7 and 10 are out of phase so to speak. While both exhibit high and low points, these occur at atypical moments in the populations' history.

In contradistinction to pattern, there are interesting deviations in *level* of abundance. For example, graphs 1–3 parallel the mean curve closely. On the other hand, graph 8 obviously maintains a low density throughout even though it is quite usual as to form. Cultures 5, 6 and 11 display especially high densities at days 1740 and 2070 and are, in general, similar to each other.

Average population size for the 31 censuses is expressed with greater precision in Table 7 in which the means for the 12 *T. castaneum* and 20 *T. confusum* cultures are recorded. For *T. castaneum* the ranking of the means has the following order:

$$6>11>10>5>4=3>9>1>7>2>12>8.$$

The maximum population (no. 6) is some 40% above the minimum (no. 8). Seven populations exhibit a density above the group mean and five fall below it. Five populations (nos. 3, 4, 5, 9 and 10) are characterized by essentially similar means.

The means for *T. confusum* listed in Table 7 are much lower, of course; in fact there is scarcely any overlap between the two species. The actual difference between the maximum and minimum cultures (no. 12 minus no. 1) is less than that seen for *T. castaneum* but about the same in terms of percentage. Ten populations have means greater than the mean of the entire sample (20·9) and ten have smaller means.

SUMMARY

In this paper, replicates of *Tribolium confusum* and *T. castaneum* populations free of coccidian infection (*Adelina tribolii*) are followed in terms of their census history for 2070 days. This encompasses about 69 continuous beetle generations. From analysis of the data the following major conclusions are drawn:

(1) All populations are successful in the sense that culture extinction never occurs.

(2) *T. castaneum* persists at a higher mean density than *T. confusum* when both are unparasitized.

(3) When parasitic infection is present, *T. confusum* is but slightly affected while the mean density of *T. castaneum* suffers some 60% reduction.

(4) *T. castaneum* characteristically persists with a higher percentage of larvae and pupae and a lower percentage of imagoes than does *T. confusum*.

(5) *T. castaneum* exhibits a marked fluctuation pattern in terms of total density. *T. confusum* also displays this but it is of lesser magnitude. It is concluded that the fluctuations result from the operation of intraspecies density-dependent factors and not from systematic alteration of the external, physical environment.

(6) In general, the means for grouped replicates afford a reasonable appraisal of the census pattern described by individual cultures.

REFERENCES

Allee, W. C., Emerson, A. E., Park, O., Park, T. & Schmidt, K. P. (1949). 'Principles of animal ecology.' Philadelphia, etc.

Bhatia, M. L. (1937). 'On *Adelina tribolii*, a coccidian parasite of *Tribolium ferrugineum* F.' Parasitology, 29: 239–46.

Holdaway, F. G. (1932). 'An experimental study of the growth of populations of the "flour beetle" *Tribolium confusum* Duval, as affected by atmospheric moisture.' Ecol. Monogr. 2: 261–304.

Park, T. (1948). 'Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst.' Ecol. Monogr. 18: 265–307.

Park, T. & Burrows, W. (1942). 'The reproduction of *Tribolium confusum* Duval in a semisynthetic wood-dust medium.' Physiol. Zoöl. 15: 476–84.

Park, T. & Frank, M. B. (1948). 'The fecundity and development of the flour beetles, *Tribolium confusum* and *Tribolium castaneum*, at three constant temperatures.' Ecology, 29: 368–74.

Steinhaus, E. A. (1949). 'Principles of insect pathology.' New York.

NATURAL POPULATION FLUCTUATIONS OF *URCEOLARIA MITRA* (PROTOZOA, PERITRICHA) EPIZOIC ON FLATWORMS

By T. B. REYNOLDSON
Zoology Department, University College of North Wales, Bangor

(With 2 Figures in the Text)

CONTENTS

	PAGE
1. Introduction	106
2. The structure, habits and life history of *Urceolaria mitra*	106
3. The flora and fauna of the College Pond	108
4. Field and laboratory methods	109
5. General account of the urceolarian population	110
6. Seasonal variations in abundance of *Urceolaria mitra*	111
(*a*) General features	111
(*b*) Relationship to physical factors	111
(1) Rainfall	
(2) Temperature	
7. Seasonal variations in the size of *Urceolaria mitra*	114
8. The urceolarian population of individual flatworms	115
9. Acknowledgements	116
10. Summary	116
References	117

1. INTRODUCTION

Urceolaria mitra von Sieb is a freely moving peritrichous protozoan found on flatworms, particularly *Polycelis* species, and belongs to the same family as the classical *Trichodina pediculus* of similar habit on *Hydra*. It has been reported most frequently by Continental workers and was described by Claparède & Lachman (1858–60) under *Trichodina mitra*, by Wallengren (1897*b*) and more recently by Peshkowsky (1923) again under *T. mitra*. Latterly, Fauré-Frémiet (1943) has reviewed the family Urceolaridae. Apparently there is no British record of this protozoan, the only reference to the urceolarians of flatworms being that of Whitehead (1915) who found *T. steinii* on a turbellarian species. Flatworms with *Urceolaria mitra* were found in the Bangor district (Reynoldson, 1947) and, although interest first centred on host specificity, the peritrich provides such suitable material that the scope of the work has been widened to a population study of the epizoic habit. Suitable data are easily obtained since the organisms occur on the flat, outer surface of triclads, especially on *Polycelis tenuis* Ijima (Reynoldson, 1948). The wide distribution and abundance of flatworms also ensure a plentiful supply of material in an assortment of habitats. Furthermore, *Polycelis* spp. are hardy laboratory organisms and give plenty of scope for experimental work, while their physiology has been much studied.

This paper is mainly descriptive and records the weekly fluctuations over one year of the population of *Urceolaria mitra* infesting *Polycelis tenuis*. All the data were collected from a small pond in the grounds of the Memorial Buildings, Bangor, where the peritrich was originally discovered. Variations in the number and also in the size of the organism have been examined in relation to temperature and rainfall. The fluctuations in the population were relatively small compared with free-living organisms and may result from the epizoic habit. The analysis has indicated that rainfall rather than temperature is implicated in the regulation of the population. High populations were usually found following periods of rain, and in the particular year of study these two factors acted in opposition as they would usually tend to do in our climate. Temperature appears to have a marked influence on the size of the peritrich but other less obvious factors may also be involved here. High temperature caused a decline in size, a feature which has been noted for Protozoa in laboratory experiments. The general level of abundance occurring on two other species of flatworm living in the pond has been recorded and reveals interesting features of host specificity.

2. THE STRUCTURE, HABITS AND LIFE HISTORY OF *URCEOLARIA MITRA*

These fascinating peritrichs, once taken to represent the medusa stage of *Hydra* (Agassiz, 1850) have attracted much attention, and a good account of the

family is given by Wallengren (1897 *a*, *b*). Other important papers dealing with the structure of individual species are those of Clark (1866) on *Trichodina pediculus*, Fulton (1923) on *T. urinicola*, Fantham (1930), Mueller (1932, 1937, 1938), and Padnos & Nigrelli (1942) on various species of *Trichodina* parasitizing fish. Recently, Hirshfield (1949) has described two new urceolarians from American limpets. A good account of the earlier taxonomy is given by Fulton. The family was formerly divided into three genera, *Trichodina*, *Cyclochaeta* and *Urceolaria*, but more recently Fauré-Frémiet (1943) has reduced the genera to two, *Trichodina* and *Urceolaria*, each with a subgenus, *Cyclochaeta* and *Leiotricha* respectively. In this paper Fauré-Frémiet is followed.

the expanded condition (Fig. 1 *a*). The adoral or anterior end is surrounded by a circlet of large cilia which lead into a vestibule set at an oblique angle to the longitudinal axis—this is particularly apparent in fixed specimens. The aboral or posterior end is also surrounded by a circlet of cilia which acts as the organ of locomotion when the organism is free-swimming and also probably while it is gliding over the surface of its host. Apart from these two circlets, cilia are absent. The striated ring lying anterior to the skeletal ring together with the latter undoubtedly form an organ of adhesion and the peritrich is able to attach itself sufficiently firmly to a glass surface to withstand a fine jet of water, just as Mueller (1938) noted for *Vauchomia* (*Trichodina*) *nephritica*. Maclennan's

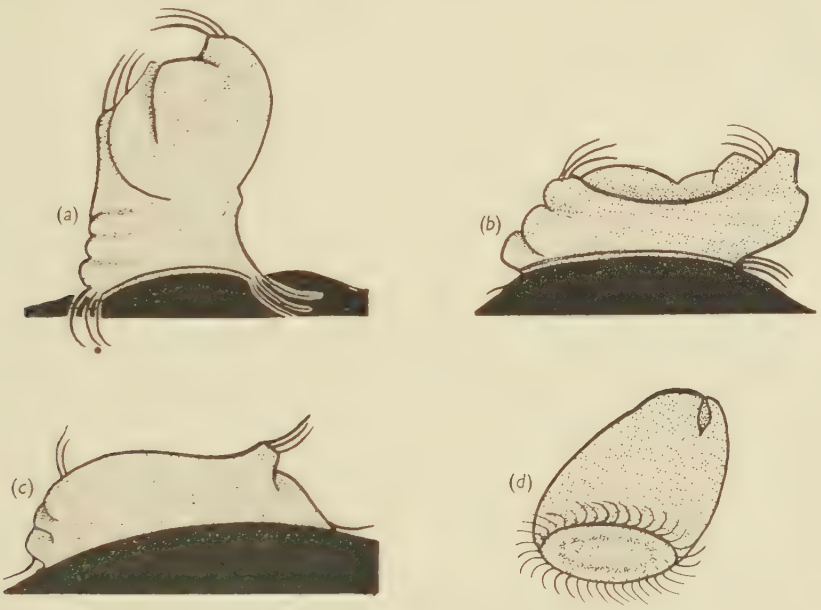


Fig. 1. Characteristic shapes of *Urceolaria mitra* (*a*) during feeding; (*b*) preparing to move; (*c*) during movement; (*d*) free-swimming individual.

The two genera are distinguished by the presence of a denticulate skeletal ring in *Trichodina* and a smooth ring in *Urceolaria*. According to Hirshfield eleven species of *Urceolaria* have been recorded, all from invertebrates. Nine occur on marine hosts, one on a land snail and *U. mitra* on flatworms.

Only a bare outline of the structure of *U. mitra* is necessary here; for detailed accounts readers are referred to the papers of Wallengren, Peshkowsky and Fulton mentioned above. This species is a comparatively large member of the family and the complicated aboral disk of an average-sized specimen measures 49 μ when fixed, but may expand to approximately twice this in the flattened position (Fig. 1 *c*). The height of a fixed specimen is 86 μ in

(1939) objection to the use of the term 'sucking disk' is therefore invalid. Like other urceolarians, the appearance of *U. mitra* is extremely variable and Fig. 1 records a series of outline drawings of characteristic shapes.

There is little in the literature on the life cycle and reproduction of *Urceolaria mitra* but reproduction in *U. patellae* is described by Caullery & Mésnil (1915) and also by Brouardel (1936, 1941) who is making an extensive study of its biology. It appears that binary fission is the main mode of multiplication, and Fulton (1923) gives a good account of the process in *Trichodina urinicola*. Conjugation is a much rarer occurrence and is anisogamous, in outline resembling the process in *Vorticella*. The reproductive behaviour

of *Urceolaria mitra* has not been examined in detail, but it is apparent that in this species conjugation is infrequent. Although several cases of *U. mitra* undergoing binary fission have been seen, no cases of conjugation have been noted in many hundreds of specimens examined during the year, except for five pairs in conjugation noted on 9 July 1949.

The life history has no complications, and resting stages have not been observed in any species of *Urceolaria*. This aspect and the habits of *U. mitra* will be more fully discussed in a paper dealing with the dispersal of the peritrich. *U. mitra* has been recorded previously from the following flatworms: *Polycelis nigra*, *P. cornuta*, *Dugesia* (*Planaria*) *lugubris*, *D. polychroa*, *D. torva* and *Dendrocoelum lacteum*. In the present work *Urceolaria mitra* has been found on *Polycelis tenuis*, *P. nigra*, *P. cornuta* and also *Dugesia lugubris*, but no special effort has been made to extend the list of hosts. The incidence and size of the peritrich population is very different for these species (§ 5).

Urceolaria mitra invariably occurs on the dorsal surface of the flatworm—only occasional individuals are found on the ventral surface, and these after the worm has been crawling on the water film in an inverted position. A study of the dispersal of this organism within a community of flatworms has shown that it is achieved by a small population becoming planktonic. But the maximum period of free life is only a few hours. This is contrary to the evidence of Kelser (1921) who never found *U. mitra* separate from its host. Brouardel (1947) has noted that *U. patellae* rarely abandons the gills of a healthy limpet.

3. THE FLORA AND FAUNA OF THE COLLEGE POND

The pond was constructed to serve an ornamental purpose in the College grounds and its basin has been dug out of rock. It measures 18 ft. in length and is 12 ft. broad, reaching a depth of $2\frac{1}{2}$ ft. Its edges are constructed of stone slabs and its sides are sheer. The pond is fed by a small stream originating from a spring which runs mostly underground, but it emerges to run down a rock face some 50 ft. high before entering the pond. The stream first enters a subsidiary basin 3 ft. across and trickles gently into the pond over a sill. Its outlet is via another sill so that the flow of water through the pond is very gentle and further hindered by dense vegetation. No current can be detected along the edges of the pond. There is a deposition of mud and silt at the entrance from where the depth of water increases steadily to the centre, becoming shallower again at the outlet. The stream shows relatively small fluctuations in volume and during the very dry spell of August–September 1947 it continued to run. Analysis of the water gave the following results:

pH	8·25	Hardness	(Wanklyn)
Dissolved solids	25·40*	Total	15·5*
Ca	1·59*	Permanent	13·0*
SO_4	5·20*	Temporary	2·5*
Cl	3·30*		

* Parts per 100,000.

The pond is heavily shaded by trees and only receives sunlight during the summer months in the early morning, thus temperature fluctuations are small (Fig. 2). It was frozen for a few days during the cold snap in February 1947, while the maximum temperature (daily average) recorded was 16·9° C. during August 1947. There is a profuse emergent and semi-emergent vegetation during the summer. At the inlet and outlet areas watercress (*Nasturtium officinale*) is abundant, while the centre of the pond is occupied by water lilies (*Nymphaea* sp.). Here and there grow patches of great spearwort (*Ranunculus lingua*) and great willowherb (*Epilobium hirsutum*). One small area of creeping scirpus (*Scirpus lacustris*) occurs at the outlet end. The marginal areas of the pond are completely covered with duckweed (*Lemna minor*) during this season. The only border plant is a patch of yellow flag (*Iris pseudacorus*) to one side of the outlet. Submerged vegetation is also abundant, consisting mainly of *Elodea canadensis*. During the summer this is mixed with a heavy growth of *Cladophora* sp. Many sycamore leaves fall into the pond and decay during the autumn, and after gales. Apart from periodic removal of watercress the pond has not been interfered with during this work.

The fauna has not been studied in detail and only the more numerous, typical organisms are mentioned. The protozoan population is varied. It is clear that holozoic forms are numerous and peak periods of *Vorticella* spp. and *Spirostomum ambiguum* have been noted during the summer months. *Hydra* spp. are very numerous during the summer, particularly on the under-surface of lily and sycamore leaves, but no specimens of *Trichodina pediculus* have been found on them. Nematodes have only been infrequently seen and have not been identified, but the pond is 'alive' with flatworms.

The most abundant worm is *Polycelis tenuis* Ijima, a species not hitherto recognized in Britain (Reynoldson, 1948), but frequently described from Europe. It is readily distinguished from *P. nigra* by its mottled colour pattern in addition to internal differences (see § 5). *P. nigra* Ehrbg. also occurs but in much smaller numbers and it apparently favours the inlet area.

As a result of observations by Dr Y. Melander (private communication) it now seems probable that

the *P. tenuis* population described in this paper included a minority of hybrids between *P. tenuis* and *P. nigra*. However, it has been established that the urceolarian populations of both flatworms are similar and for the purposes of this paper they can be considered together.

P. tenuis, which is found on the under-surface of fallen sycamore leaves, under lily leaves and amongst the *Elodea*, exists in such vast numbers that a small piece of worm used as a bait attracts 200–300 individuals in about 15 min. It is difficult to obtain a numerical estimate but using bait at a number of points suggested that the total population exceeds 20,000 so there was no danger of depleting the population by weekly removals of 20 individuals. *Dugesia lugubris* O.Sch. was also very abundant and collections by bait indicated that they rivalled *Polycelis tenuis* numerically. They seemed to live at a slightly deeper level in the pond than *P. tenuis*. Single specimens of *P. cornuta* (Johnson) and *Phagocata* (*Fonticola*) *vitta* Dugés have also been taken.

The most conspicuous oligochaete is *Lumbriculus variegatus* (Müll.) occurring around the pond margins among decaying leaves. No other species have been noted except *Chaetogaster limnaei* v. Baer from *Limnea pereger*, and a *Naidium* sp. but they probably occur. *Helobdella stagnalis* (L.) is common and the only leech recorded. The most abundant mollusc is *Limnea pereger* (Müll.) and it has a well-marked peak in the late summer, whilst *Ancylus lacustris* Linn. is also very numerous on the under-surface of lily leaves. *Hydrobia jenkinsi* Smith and *Planorbis complanatus* L. also occur.

The water is particularly rich at times with plankton in which *Simocephalus vetulus* (Müll.) and *Acanthocyclops viridis* (Jurine) dominate. *Cypricercus affinis* (Fischer) is a common ostracod of the substratum of decaying vegetable material. *Asellus meridianus* Racovitza is extremely numerous, on every leaf, and is the organism which occurs in greatest bulk. *Gammarus pulex* has not been taken. There is also a restricted fauna of insects. The stone-fly nymph *Nemurella inconspicua* (Pict.) is common, and an ephemeropteran has been seen in abundance at times but was absent during the current collection. Only two beetles have been found, namely adults of *Haliplus lineatocollis* (Marsh.) and *Agabus bipustulatus* (L.) together with larvae of *Agabus* sp. Three species of Diptera have been collected, adults of *Limnophora exsurda* Pandellé and larvae of *Tanypus* sp. and *Dixa* sp. The surface bug, *Velia currens* (Fab.), has a short summer season but corixids have not been observed since 1946 when Mr J. Hobart found *Corixa nigrolineata* (Fieb.) and *C. sahlbergi* (Fieb.). The mite *Arrhenurus zachariasi* Koen. is very abundant. Apart from the annual visits of breeding frogs (*Rana temporaria* L.) aquatic vertebrates are absent—there is usually a large, temporary population of tadpoles.

The dominant bottom forms are thus *Polycelis tenuis*, *Dugesia lugubris*, *Lumbriculus variegatus*, *Limnea pereger* and *Asellus meridianus*.

4. FIELD AND LABORATORY METHODS

An intensive study of a single habitat was favoured rather than an extensive examination of a variety of habitats to provide such data for *Urceolaria mitra* as the seasonal trend in numbers, size and reproductive activity, particularly in their relation to seasonal factors such as temperature and rainfall. It also gave a more intimate picture of the incidence of the peritrich and the population carried by individual worms.

The population of *U. mitra* was determined from weekly samples of 20 flatworms collected two each from ten stations. The sampling was random in that the first two worms seen at each station were taken. They were so numerous on the undersides of leaves that the two nearest an edge were chosen. They were brought to the laboratory in small tubes each containing one worm and counting was started at once. The worms were first transferred to a Petri dish where colour and length were noted. Only the broadest categories were used for colour, namely black, brown or grey, as it appeared to the unaided eye. These categories were further split into dark, light or very light. The length was measured in mm. to the nearest 0·5 mm. while the worms were extended during normal crawling movement. For quick removal of the urceolarians from the surface of the flatworm without damaging the latter, immersion in 0·02% chromic acid on a well-slide proved adequate. In about 10 min. the *Urceolaria* had dropped off and could be counted with ease under a binocular microscope. After practice 20 worms could be dealt with in this way in 1½ hr. The sampling extended over 12 months from December 1946 with gaps amounting to 4 weeks. Twenty worms were used to estimate the protozoan population because it was the maximum number that could be dealt with in the time available. At a later date the suitability of this number was examined statistically to determine whether any increase or decrease could be justified because a balance must be struck between accuracy and labour involved when sampling populations. For this purpose the variance of a single count has been estimated from a sample of 100 worms. The mean of this sample was 37·27 and the variance 381·57 giving the standard error of a single count as 19·53. The width of the fiducial range of the mean has been calculated for various sample sizes. It shows that an appreciable increase in accuracy could have been obtained only by a relatively large increase in the

sample. This was not considered to be justified in the preliminary work.

It is unnecessary to consider the influence of variation in worm size on the peritrich population in relation to sampling because the two are usually independent except for worms which have recently hatched. Size can be ignored for worms more than 4·0 mm. in length (see § 8).

The skeletal ring proved suitable as an indicator of the relative size of individual urceolarians as it was free from shrinkage when treated with reagents, and visible in any position of fixation. The only complication was the presence of two rings during the early stages after fission (Fulton, 1923) but this condition was rarely encountered.

The technique finally adopted was to take the urceolarian population of the first and every fifth worm in the sample of twenty, remove the excess chromic acid from the well-slide with absorbent paper, fix in 70% alcohol and stain in dilute methylene blue for a few minutes, then clear in xylol. The diameter of the skeletal ring was measured with a ×6 Zeiss micrometer eyepiece. The purpose of the methylene blue was to make the protozoans obvious and to bring out clearly the yellow ring which did not stain. Little harm was done if the urceolarians were left in any stage overnight. During periods of scarcity of *U. mitra* additional worm populations were included to increase the number of *Urceolaria*. A total of 3803 with a weekly average of 78 was measured.

5. GENERAL ACCOUNT OF THE URCEOLARIAN POPULATION

The urceolarian populations of the three species of flatworm found habitually in the pond are very different and will be dealt with in turn. *Polycelis tenuis* is the species with the largest and most persistent population of *Urceolaria mitra*, and the data for 930 worms collected during the period of the investigation are shown in Table 1.

Table 1. *Comparison of the urceolarian populations of the three species of flatworm grouped for the period December* 1946 *to November* 1947

No. of *Urceolaria mitra* on individual worms ...	0	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90
Frequency for *Polycelis tenuis*	23	225	254	177	129	73	36	24	7	2
Frequency for *Polycelis nigra*	21	14	0	0	0	0	0	0	0	0
Frequency for *Dugesia lugubris*	244	26	0	0	0	0	0	0	0	0

The average population of *U. mitra* per worm over the 12 months was 22·7. The maximum recorded from one worm in the weekly counts was 85 but an individual with 100 *Urceolaria* was taken in the special sample referred to in § 4. Twenty-three worms (2·5% of total) had no epizoites while half the worms had less than 25 *U. mitra*. If an average-sized worm of 7·0 mm. is taken, then the average population of *U. mitra* (22·7) covered about 5% of the dorsal surface, allowing for variation in shape, while 100 average-sized *Urceolaria* covered about 25%. It is clear that there was plenty of space for the increase of the peritrich population.

Worms without *Urceolaria* were derived from two sources. Undoubtedly some of them were recently hatched individuals which had not yet become 'infested' while others were adults from which the epizoites had either migrated or died off during a period of population depression (see § 8). Early in the work it appeared possible that the intensity of pigment in the worms was related in some way to the peritrich population. This matter arose because *Polycelis nigra* and *Dugesia lugubris* are both heavily pigmented forms and are also relatively free from *Urceolaria mitra*. Accordingly, the worms were divided into two colour groups, the 'black varieties' and the 'very light brown' forms—intermediate shades were not considered. The average population of the 'dark' variety was 22·7, of the light 19·8. The difference between the means is 2·9 while the standard error of this difference is 2·075. Thus there was no significant difference in the urceolarian populations of these extreme colour varieties and the data suggest that the amount of pigment does not influence the population of *U. mitra*.

Attention had early been directed to an apparent colour variety of *Polycelis nigra* because they were usually without *Urceolaria*. These forms had only one shade of pigment, usually black or grey, which was uniformly distributed in contrast to the more usual mottling of darker and lighter browns or brown and grey. Such uniformly coloured varieties proved to be *Polycelis nigra* while the mottled forms agreed with the description of *P. tenuis* Ijima. As Komárek (1926), Sekera (1927) and Lender (1936) have shown recently, there are distinct anatomical differences particularly in the structure of the penis and the presence or absence of musculo-gland organs. Although most recent European opinion takes the view that externally the two species cannot be distinguished and that their ecology is similar, there is no doubt that British specimens which have been collected can be distinguished by colour pattern. Evidence is accumulating that their ecology and physiology also differ. In the field it is difficult to

distinguish them (this also applies to young worms $<3{\cdot}5$ mm. in the laboratory) and *P. nigra* has been taken in the weekly collections. It appeared 35 times so that the proportion of *P. nigra* to *P. tenuis* in the pond is approximately 1 : 25·1; but *P. nigra* may be more abundant near the inlet. The epizoic population of *P. nigra* is recorded in Table 1; it was either nil or very small. Twenty-one (60%) of the 35 specimens had no *Urceolaria*, the maximum population was four and the average 0·69 per worm. Thus the host specificity is fairly clearly defined but its basis cannot be considered here.

Earlier, it was reported that *Dugesia lugubris* did not carry the epizoite and the preference for *Polycelis tenuis* was confirmed experimentally (Reynoldson, 1947). Accordingly, only five *Dugesia lugubris* were examined at fortnightly intervals, but when a worm was found infested with *Urceolaria mitra* in June a collection of fifty worms was examined. Twelve of these carried single individuals of *U. mitra*, one had two and another five, the remaining thirty-six were negative. Thereafter ten worms were examined weekly. This apparent overflowing of the peritrich population from its usual host *Polycelis tenuis* on to *Dugesia lugubris* lasted only a short while and occurred at the time of its maximum abundance. The peak infestation was such that 75% of the population of *D. lugubris* were infested but it remained light (Fig. 2). A minor overflow also occurred in November 1947 when *Urceolaria* was recovering from its August eclipse. It seems unlikely that the peritrich bred on *Dugesia lugubris*, and Table 1 shows that of the 270 examined during the year 246 carried no *Urceolaria mitra*, while of the 26 positive records 18 were of individual urceolarians. The average number per worm was only 0·17. This epizoic population either dies out when not constantly renewed or returns to *P. tenuis* as soon as there is a decline in numbers. The phenomenon is interesting in view of Thorpe's (1945) paper on ecological isolation and species formation, particularly if the event occurs periodically as seems likely. It suggests how a new species of *Urceolaria* might arise.

Various other organisms in the pond likely to harbour *U. mitra* have been examined from time to time but *Hydra* sp., *Helobdella stagnalis* and *Limnea pereger* have all proved negative; a solitary tadpole out of twenty-two examined was found with a single specimen of *Urceolaria mitra* on its gills.

6. THE SEASONAL VARIATIONS IN ABUNDANCE OF *URCEOLARIA MITRA*

(*a*) *General features*

In considering abundance, the size of *U. mitra* is a related factor but only of minor importance and it has been omitted from the discussion, but its influence is taken account of in the partial correlations (see § 6*b*). The seasonal fluctuations in the population of *U. mitra* infesting *Polycelis tenuis* are recorded in Fig. 2 on a weekly basis as the average population per worm. The peritrich is active throughout the year and in this it differs from a large number of free-living forms which endure unfavourable periods in an inactive state. Possibly the absence of a resistant stage in *Urceolaria mitra* is related to the use it makes of its host throughout the year as a means of transport in seeking food. Unlike many other hosts the flatworm is available at all seasons. The other general feature of the population is the low range of the fluctuations—the minimum average was 2·5 peritrichs per worm and the maximum was 44, giving a range of 1 : 17·6 which is low compared with free-living aquatic Protozoa. For example, Wang (1928) records from a pond a minimum range of 1/20 (*Holophrya gargamella*), a maximum of 1/225 (*Halteria grandinella*) and an average for the Infusoria of 1/72. This stability may result from the epizoic habit of *Urceolaria mitra* which provides new feeding areas with a minimum expenditure of energy. Both persistence and relative stability of the population may be advantages which result from the habit of living on flatworms. Brouardel (1941) records a similarly low range (1 : 14·7) for the seasonal variation of *U. patellae*, but the infestation of limpets was much higher than of the flatworms.

(*b*) *Relationship to physical factors* (Fig. 2, Tables 2 and 3)

There are no obvious seasonal differences in the population level of *Urceolaria mitra*; high and low levels occur apparently independently of the season. The peak was reached in May and June, and the lowest level, persisting for 6 weeks, occurred during August–September 1947 during a particularly hot, dry period. It was then that 12 of the 23 void records on *Polycelis tenuis* occurred. The population trend has been examined in relation to two factors, temperature which Wang (1928) reported as outstandingly the most important single factor influencing the numbers of Protozoa in ponds, and rainfall. Other factors such as pH, which lay within limits of 7·5–8·5 and oxygen tension which was high, seemed unlikely to vary sufficiently in the College pond to exert a major influence.

(1) *Rainfall.* The importance of rainfall was not appreciated until the work had progressed for some months. The only records available were taken at Aber village, which is 5 miles along the coast to the east of Bangor. It has been ascertained, however, that the rainfall at Aber and Bangor has the same pattern and only minor differences will occur. The average rainfall for the week preceding the urceolarian

Table 2. *The average pond temperature and rainfall for the 7 days preceding the recorded date*

The average number of *Urceolaria mitra* per worm, the average and maximum size of the skeletal ring are recorded against the date of collection. The percentage infestation of *Dugesia lugubris* is based on the examination of five worms where shown in italics, otherwise on ten.

Date	Av. temp. (° C.)	Av. rainfall (in.)	*Urceolaria mitra* Av. no. per worm	*Urceolaria mitra* Av. size (μ)	*Urceolaria mitra* Max. size (μ)	Percentage of *Dugesia lugubris* infested
1946						
2 Dec.	9·4*	0·13	41·4 ± 3·95	—	—	*0*
10 ,,	5·5*	0·21	42·2 ± 4·34	40	50	—
16 ,,	7·7*	0·33	38·2 ± 3·67	40	50	—
23 ,,	4·0*	0·14	—	—	—	—
31 ,,	7·0*	0·15	29·5 ± 2·45	39	50	—
1947						
6 Jan.	7·2*	0·30	17·6 ± 2·66	37	50	*0*
13 ,,	7·0*	0·30	18·7 ± 2·47	36	45	*0*
20 ,,	7·7*	0·37	20·8 ± 2·94	37	49	*0*
27 ,,	2·2*	0·02	24·0 ± 2·33	36	46	*0*
3 Feb.	0·0*	0·02†	16·7 ± 1·90	37	48	*0*
10 ,,	0·0*	0·05†	15·8 ± 1·63	39	46	*0*
17 ,,	0·5*	0·0†	17·5 ± 1·67	39	49	*0*
24 ,,	−1·0*	0·01†	17·7 ± 2·28	39	53	*0*
3 Mar.	0·5*	0·13†	16·7 ± 1·90	40	53	*0*
10 ,,	6·4‡	0·14	21·7 ± 3·13	40	49	*0*
17 ,,	6·3‡	0·27	24·2 ± 2·68	42	53	*0*
24 ,,	7·7‡	0·35	34·1 ± 3·62	41	53	*0*
31 ,,	8·3	0·10	39·4 ± 3·24	39	56	*0*
6 Apr.	7·7	0·15	—	—	—	—
14 ,,	8·3	0·23	22·6 ± 2·60	39	52	*0*
21 ,,	9·4	0·06	17·8 ± 2·56	43	46	*0*
28 ,,	9·7	0·19	16·2 ± 3·21	40	52	*0*
5 May	9·6	0·15	21·8 ± 3·15	41	48	*0*
12 ,,	11·5	0·06	22·2 ± 3·66	36	45	—
19 ,,	11·3	0·24	25·8 ± 3·61	38	46	*0*
26 ,,	13·1	0·12	38·0 ± 3·31	38	49	—
1 June	14·4	0·03	29·0 ± 4·38	37	45	—
8 ,,	13·6	0·14	38·9 ± 4·41	36	45	*20*
16 ,,	14·2	0·10	37·0 ± 5·23	36	42	30
23 ,,	14·0	0·05	35·6 ± 3·85	34	45	70
30 ,,	15·1	0·06	43·8 ± 3·29	35	45	40
7 July	13·8	0·07	32·5 ± 2·71	34	43	50
14 ,,	13·4	0·03	31·0 ± 4·04	35	43	20
21 ,,	14·9	0·09	37·3 ± 4·08	35	42	20
25 ,,	14·9	0·04	25·1 ± 3·42	35	43	—
31 ,,	16·1	0·10	—	—	—	—
5 Aug.	16·1	0·08	—	—	—	—
12 ,,	15·8	0·0	5·4 ± 1·37	33	40	0
18 ,,	16·3	0·0	5·0 ± 1·10	34	40	0
25 ,,	16·5	0·0	3·5 ± 0·99	32	37	0
1 Sept.	16·5	0·0	2·6 ± 0·86	36	40	0
8 ,,	15·3	0·1	2·4 ± 0·48	35	46	0
15 ,,	15·2	0·26	7·1 ± 1·11	35	39	0
22 ,,	14·9	0·13	8·5 ± 1·38	33	40	0
29 ,,	14·1	0·12	14·8 ± 2·27	35	40	—
6 Oct.	13·6	0·0	10·5 ± 1·25	35	42	0
13 ,,	13·9	0·08	13·6 ± 2·04	36	44	0
20 ,,	13·0	0·01	17·1 ± 2·48	37	45	0
27 ,,	11·8	0·02	18·2 ± 2·23	36	43	—
3 Nov.	11·8	0·07	21·1 ± 2·45	37	46	10
10 ,,	11·7	0·16	24·7 ± 3·76	38	51	0
17 ,,	10·0	0·32	23·7 ± 3·32	38	45	10
24 ,,	10·3	0·27	24·5 ± 3·42	38	46	*0*
1 Dec.	8·2	0·08	23·3 ± 2·61	36	42	0

* Air temperature.

† Snow.

‡ Air temperatures for these 3 weeks were 1·7, 4·4 and 8·3° C. respectively.

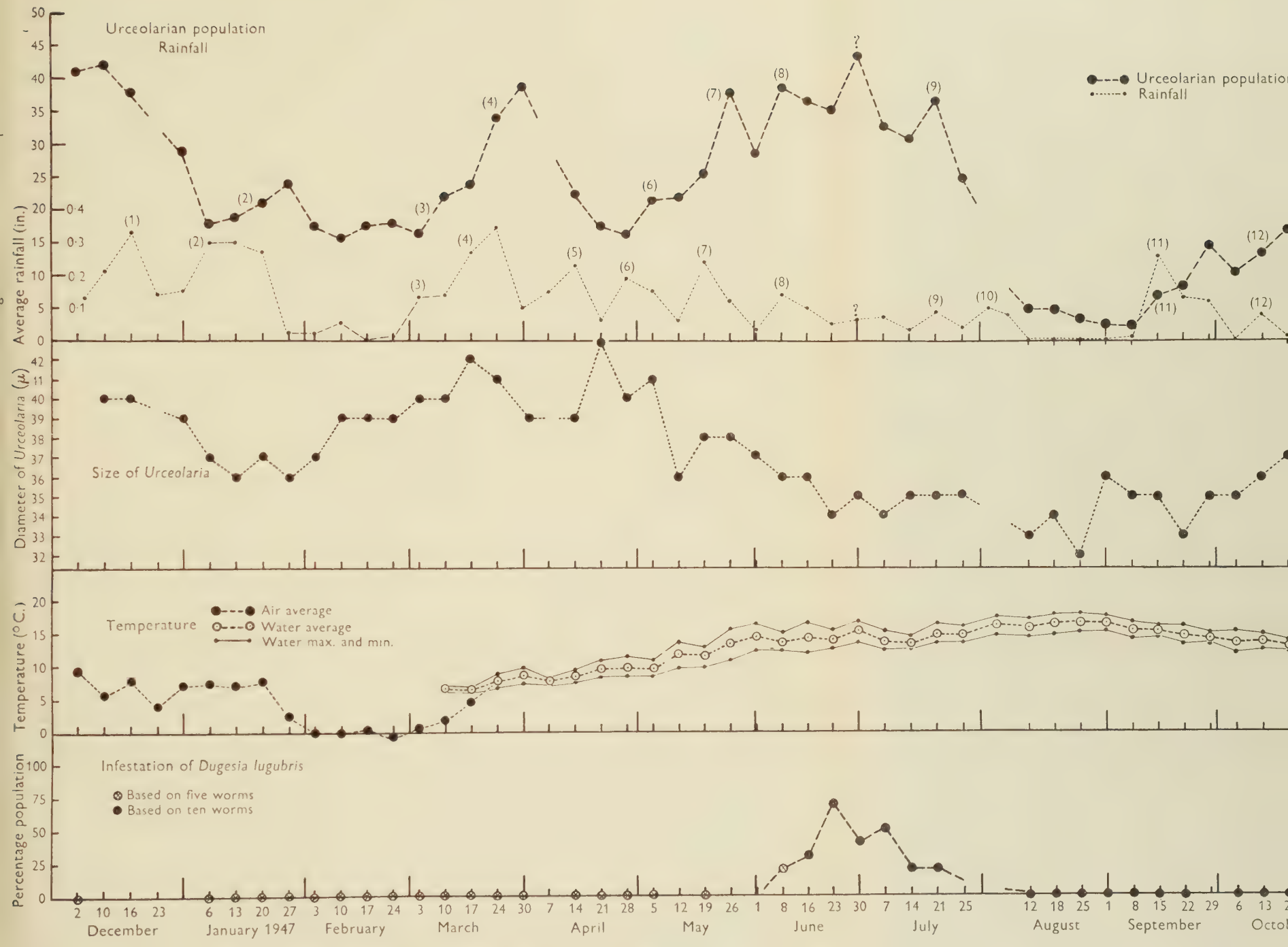


Fig. 2. Average population of *Urceolaria mitra* on *Polycelis tenuis*; average size of *U. mitra* (= skeletal ring) and incidence on *Dugesia* (*Planaria*) *lugubris*.

estimate is plotted in Fig. 2. The periods of increase in rainfall are numbered (1) to (13) in Fig. 2—clearly such an arrangement is arbitrary and relative but it assists the initial examination of the data. Peaks (1) and (10) are not considered further because data for the urceolarian population of the following week are not available. From the commencement of the observations on 2 December 1946 until 12 May 1947, with one exception, the rainfall peaks are followed by an increase in the peritrich population the week after; the exception (no. 5) will be discussed later. From 12 May to approximately 13 October the rainfall peaks coincided with an increase in *Urceolaria mitra* during the same week. The apparent relationship between rainfall and abundance of *Urceolaria* is particularly well brought out by the dry spell during August when the population was depressed. Following the rain in September the urceolarian population began to increase. The outstanding exception (no. 5) is interesting because, although the total rainfall for the week ending 14 April was 1·60 in., 1·37 fell on the first day of the week and thereafter it was small until 20 April. Thus the decline in *Urceolaria* instead of the expected increase might be due to the time interval between rainfall and sampling—13 days. This was the only occasion on which the maximum interval between heavy rain and sampling occurred. There are minor discrepancies between rainfall and population during September and October, but these may be due to the general recovery of the population after the abnormally dry spell in August and early September.

The correlation between rainfall and the urceolarian population has been examined statistically over the period 7 March 1947 to 1 December 1948. (The shorter period was taken because temperature records were available only from 7 March.) From the earlier date to 12 May and from 27 October to 1 December rainfall was related to the urceolarian population of the following week—over the remainder of the period it was related to the population of the same week. The criterion used for this splitting is based on the change over during May when the average weekly temperature of the week in which it occurred was 12·5° C. So during periods when the temperature was below 12·5° C. rainfall was related to the population of the following week—above, to that of the same week. A correlation coefficient of 0·337 ($n=37$, $P<0·05$) was obtained, which is significant. Over the full 12 months, rainfall and the urceolarian population are still significantly related. Although the correlation relates absolute rainfall to abundance, it is not suggested that the relationship is so straightforward as this. The observation that the highest level of *U. mitra* was reached during May, June and early July when the rainfall was not particularly high is a pointer that other factors modify the influence of rainfall. For example, the effect of temperature on the general activity of *Polycelis tenuis* may be expected to influence the urceolarian population.

(2) *Temperature.* Records of water temperature in the pond are available only from 7 March but for the earlier period air temperatures are also shown in Fig. 2. It seems clear that no simple relationship existed between temperature and abundance of *Urceolaria mitra*. During the early summer the rise in the population coincided with the rising temperature, but during the warmest period of August the population declined. Again, the autumn increase in *U. mitra* occurred at a time of declining temperature. It is to be anticipated that both rainfall and temperature would react on the urceolarian population and the clearest method of analysis is by means of correlation coefficients. These, including partial correlations, are recorded in Table 3 for the various relationships examined.

The correlation coefficient relating temperatur and the abundance of *U. mitra* is not significant ($r=0·292$, $0·1>P>0·05$) and the negative sign of the coefficient emphasizes this anomaly because there is no doubt that the physiological effect of increasing temperature within the limits recorded from the pond

Table 3. *The value of the correlation coefficients for the relationships discussed in* §§ 6 *and* 7 *calculated over the period* 7 *March to* 1 *December* 1947

Significant correlations indicated by asterisks * $0·05>P>0·01$; ** $P<0·01$.

Relationship	r ($n=37$)	Eliminated in calculating partial correlations: Abundance	Temperature	Rainfall	Size	Eliminated in pairs
Abundance-rainfall	+0·337*	—	+0·346*	—	+0·343*	Temperature and size, +0·441**
Abundance-temperature	−0·292	—	—	+0·164	−0·138	Size and rainfall, +0·323
Rainfall-temperature	−0·880**	—	—	—	—	
Size-abundance	+0·255	—	+0·100	+0·084	—	Rainfall and temperature, +0·122
Size-temperature	−0·616**	−0·586**	—	−0·515**	—	Abundance and rainfall, −0·544**
Size-rainfall	+0·452**	+0·442**	−0·241	—	—	Abundance and temperature, −0·295

is to increase the potential reproductive rate of Protozoa. More particularly, Brouardel (1946) reported that within limits of 8–16° C., increase of temperature markedly shortened the duration of division in *U. patellae*. There are no corresponding data for *U. mitra*. From the positive sign of the coefficient for rainfall and abundance and the negative sign for temperature and abundance it would seem that these two factors or others related to them acted upon the peritrich population in opposition. How this can have happened is made clear by the highly significant but negative correlation between rainfall and temperature for this particular year ($r = -0{\cdot}880$, $P < 0{\cdot}01$). It is probably due to this contrast that the relation to rainfall has stood out so well. The partial correlations show that in this 'pull' between rainfall and temperature the former was more closely related to abundance. It would appear that rainfall or some associated factor is the first essential for increase in the population of *U. mitra* and that multiplication will occur at fairly low temperatures. However, as already noted, the reaction may then be retarded. If temperature and rainfall 'pull' in the same direction, as happened particularly during May and, to a lesser extent in June, there is a rapid increase in the population. In hot but dry weather the population declines.

In this preliminary stage there is little profit in discussing the mechanism whereby rainfall could influence *U. mitra*, but it is significant that Taylor (1940), in his studies on the bacterial flora of Windermere, found rainfall and the bacterial population to be positively correlated. Recently, Gray (1948) has reported a similar connexion between rainfall and the bacterial flora of a stream. If bacteria form the food of *U. mitra* as Diller (1928) reported but without giving the evidence, then the connexion may be relatively straightforward. On the other hand, high statistical correlation does not demonstrate cause and effect. Moran (1949) has also sounded a warning on the use of correlation coefficients under certain conditions, but their value as a pointer to the most profitable approach to a problem is not disputed. Field work is now in progress to study the connexion between rainfall, bacteria and *U. mitra*. In the ultimate analysis of population control it will be necessary to consider the biomass in addition to the number of organisms.

In discussing the fluctuations of the urceolarian population no allowance has been made for any influence of variations in the host population. A quantitative estimate of *Polycelis tenuis* was not attempted over the period of this work but weekly observations suggested that there was no marked seasonal trend in numbers. Data obtained by monthly counts of worms on tiles over a later 10-month period, including the breeding season, showed that the maximum population in August was 4·5 × the December minimum on a monthly basis. The average amplitude of the fluctuations was 35 % of the mean value. These observed variations are likely to be larger than actuality owing to the gregarious behaviour of the worms and seasonal changes in the substratum, etc. Thus, even assuming that the urceolarian populations of individual worms influence each other, and this may not be so, such variations in the host population are unlikely to invalidate the conclusions reached.

7. SEASONAL VARIATIONS IN THE SIZE OF *URCEOLARIA MITRA*

Since *Urceolaria* multiplies only by binary fission an increase in the population should be accompanied by a reduction in average size and the original purpose of studying size was to relate reproductive activity to abundance. There is some indication of such a relationship during the periods of abundance recorded for 30 March to 10 April and again for 19 May to 23 June. In the latter period, examination of the size stratification of the protozoan population demonstrated that the reduction in size was in fact due to the onset of fission. But over the greater period such a relationship is not apparent and is overshadowed by the larger size of *U. mitra* during the winter than during the summer (Fig. 2). It is probable that temperature, abundance and size are interrelated and rainfall may also be involved. The interaction of these factors has been examined by means of partial correlations and the results are given in Table 3.

It seems clear that size and abundance showed no relationship over the whole period ($r = +0{\cdot}255$, $P > 0{\cdot}1$) and there is no significant correlation even when the influence of temperature and/or rainfall is eliminated. But it should be noted that the positive correlation which was an unexpected result, becomes less when these abiotic factors are eliminated. It must be concluded that the average size of *U. mitra* does not necessarily give an indication of reproductive activity. This is due to the marked relationship between temperature and size—increasing temperature is accompanied by a decline in average size of *U. mitra* which is highly significant ($r = -0{\cdot}616$, $P < 0{\cdot}01$) and remains so when the influence of other factors is eliminated. Despite the lack of significant correlation between abundance and temperature or size it is still possible that the smaller summer size was due to temperature stimulating reproduction. The result might not be reflected in the population because of some adverse factor. To rule out this possibility the largest individual measured in each weekly collection was related to temperature. This gave a correlation coefficient of even higher significance ($r = -0{\cdot}970$, $P < 0{\cdot}01$).

The reduction in size of Protozoa accompanying an increase in temperature is well known from laboratory experiments, but has not been demonstrated in natural populations so clearly. Adolph (1930) has examined the factors regulating the size of Protozoa and concludes that the smaller size at higher temperatures results from an increase in fission rate relative to the assimilative rate. But the lack of negative correlation between abundance and size suggests that in *U. mitra* this is not the whole explanation. Food may also influence adult size, shortage causing a decrease (Pearl, 1906; Harding, 1937*b*), plenty causing an increase (Harding, 1937*a*), but here positive correlation with abundance would be expected. It is possible, of course, that these two opposing factors, temperature and food, acted on the urceolarian population in the particular year of observation to produce a spurious significant negative correlation with temperature. Particularly would this be the case if the August population depression was due to food shortage which in turn influenced size. As might be expected, in view of the highly significant negative correlation between rainfall and temperature, there is a significant positive correlation ($r = +0{\cdot}452$, $P < 0{\cdot}01$) between rainfall and size. But when the influence of temperature is eliminated this becomes negative and non-significant, and with the above reservations it appears that temperature exerts the dominating influence on the size of *U. mitra*.

8. THE URCEOLARIAN POPULATION OF INDIVIDUAL FLATWORMS

The data so far discussed have related to an average population per worm, but there are interesting features of the urceolarian populations of individual worms. Such a fundamental aspect of animal relations has seldom been thoroughly studied, the difficulty being the accurate determination of the epizoic or parasitic populations and the area or volume of the host. Such data are easily obtained for *U. mitra* and *Polycelis tenuis*.

The figures for individual worms were collected into monthly groups and the relationship between worm length, area and the peritrich population examined. The variation in the peritrich population of individual worms at any time is considerable and the average standard error calculated on a weekly basis over the whole period was 13·8% of the mean with limits of 7·5–33·1%. A second feature is that the smallest worms have, particularly at certain periods, a population much lower than the average, while thirdly, for worms greater than 4·0 mm. in length there is no increase in the population of *Urceolaria mitra* as the worms increase in size for each of the 12 months with the exception of June and July. This is shown clearly by the correlation coefficients for flatworm length × urceolarian population recorded in Table 4. It is only the second point for which any explanation can be offered at the moment. Work on the dispersal of *U. mitra* has shown that newly hatched worms are free of the ciliate and only after some 2–4 weeks do they become 'infested' and carry a population of average size. Thus the youngest worms will tend to have a smaller peritrich population than older worms, producing the effect noted. It is to be expected that this would reach a maximum during the breeding season of *Polycelis tenuis*. From field observations of the flatworm cocoons the peak deposition occurred during the last week in April, and at the prevailing temperature in the pond, peak hatching must have occurred at the end of May. This is supported by Table 5, which shows that the

Table 4. *The correlation between flatworm length and the population of* Urceolaria mitra *on a monthly basis*

Significant values of r indicated by asterisks ($P < 0{\cdot}01$).

Month	Average population of *U. mitra* per worm	n	r (worm length × population)	Trend of population
1946				
Dec.	37·6	68	−0·036	−
1947				
Jan.	19·6	59	−0·070	+
Feb.	16·0	69	−0·103	S
Mar.	27·2	88	+0·058	+
Apr.	18·8	58	−0·359**	−
May	27·4	74	−0·062	+
June	40·9	84	+0·331**	+
July	30·9	76	+0·421**	−
Aug.	4·9	56	−0·043	−
Sept.	7·7	82	+0·094	+
Oct.	15·0	72	+0·130	+
Nov.	23·0	97	+0·129	+

highest proportions of young worms in the routine samples occurred in May and June. Previous to observations of hatching in May it had not been possible to distinguish recently hatched worms from 'small' individuals.

Table 5

Month	No. of young worms	Total no. of *P. tenuis*	Percentage of young worms
May	6	74	8·1
June	19	84	22·6
July	2	76	2·6
August	2	56	3·6
September	4	82	4·9
October	0	72	0
November	0	92	0

Thus the presence of young worms in May and June accounts for the relatively low peritrich population of this category compared with other months. But a general tendency for the smallest worms to have a lower epizoic population suggests that sporadic breeding may occur throughout the year and this is supported by observation.

There are certain features of the relationship between flatworm size and the urceolarian population which can be discussed with advantage at this stage. Thus, if the dorsal surface of *P. tenuis* forms a uniformly suitable habitat for *Urceolaria mitra* we should expect larger worms to carry a larger epizoic fauna. But, as already noted, a positive significant correlation between flatworm length and the urceolarian population is obtained only for June and July, the period when the protozoan reached its peak abundance. Otherwise, apart from April, which showed significant negative correlation, host size and the epizoic population were independent. If the correlation coefficients are plotted against the average monthly population the regression line shows an upward trend suggesting that as the population increases so the epizoite tends to occur in greater numbers on the larger worms. Table 4 also records the trend of the average population during each month, upward trends are indicated by +, downward by − and stationary by an S. Comparison of these signs with those for the correlation coefficients showed that in eight cases they agree, disagree in three, while one inconclusive result is obtained for February. One of these disagreements is probably not important because in January the trend was barely upward. Such a high proportion of agreement, although not sufficient by statistical standards ($P = 0{\cdot}113$), suggests that not only does *U. mitra* tend to colonize the bigger worms in relatively greater numbers during high levels of abundance but may also do so when the population is increasing irrespective of the general level. However, it is only when a high level of abundance is reached that the number of ciliates *per unit area* approaches a constant value for worms of 5 mm. in length and upward.

This account of the urceolarian population of individual worms is tentative and incomplete but certain features emerge on which to base further work, namely:

(1) At low levels of abundance, particularly if the trend is declining or stationary, *U. mitra* is unable to avail itself of the greater surface area of larger worms.

(2) During periods of increase in the average population it is able to do so to a limited extent, and only when a high population level is attained does it behave as if the worm afforded a uniform habitat.

(3) (1) and (2) suggest that the dorsal surface of *Polycelis tenuis* may not afford a uniformly favourable habitat for *Urceolaria mitra*.

(4) The data also suggest that this is probably an ecological problem rather than a physiological one, and that the food supply of *U. mitra* is intimately involved.

(5) Any explanation has to cover the considerable variation in the urceolarian population of equal-sized worms at a given time.

9. ACKNOWLEDGEMENTS

I wish to thank Prof. F. W. Rogers Brambell, F.R.S., for his interest and encouragement during the work. Mr M. J. R. Healy has kindly advised me on the statistical treatment of the results, particularly in § 4. I am grateful to Dr T. T. Macan for identifying the molluscs, to Mr J. Hobart for examining the insects and to Dr J. P. Harding for naming the Crustacea. Mr R. D. Tweed assisted by naming the plants for me. Finally, I am indebted to Dr H. H. Goldthorpe who provided the data on the chemical analysis of the pond water.

10. SUMMARY

1. A brief description of the structure and biology of *Urceolaria mitra* Von Sieb epizoic on flatworms is given.

2. The habitat in which the peritrich was studied, also the field and laboratory methods of estimating population fluctuations, are described. Population data are based on weekly counts from a sample of twenty *Polycelis tenuis* Ijima.

3. An account is given of the abundance and incidence of the urceolarian population on the flatworms occurring in the pond. *Urceolaria mitra* infested mainly *Polycelis tenuis* but was also found in small numbers and low incidence on *P. nigra*

Ehrbg. and *Dugesia* (*Planaria*) *lugubris* O.Sch. The infestation of *D. lugubris* was sporadic, occurring when the peritrich population was high.

4. The seasonal fluctuations of *Urceolaria mitra* are described. The population was permanent and very stable compared with free-living Protozoa. This may result from the epizoic habit.

5. The fluctuations are discussed in relation to rainfall and temperature. Positive, significant correlation with rainfall has been found, but the reason for this is not yet known. There was no significant relationship with temperature and it was concluded that during this particular year November 1946–December 1947 rainfall had a greater influence on the urceolarian population than temperature.

6. The average weekly size of *U. mitra* has been examined in relation to abundance and temperature. There was some indication that during periods of increase the average size declined due to binary fission, but any correlation between abundance and size was masked by a marked temperature effect. There was a highly significant negative correlation between temperature and average size. This became even more pronounced when the largest individual in each weekly sample was related to the temperature, showing that it was an effect on adult size which was operating.

7. The data for the urceolarian population of individual worms has been examined. There was wide variation in worms of equal size, and no relation between the size of the worm and the epizoic population apart from 2 months when the peritrich population was at its peak. Recently hatched worms had a smaller population of *U. mitra* than older individuals.

REFERENCES

Adolph, E. F. (1930). 'The regulation of size as illustrated in unicellular organisms.' London.

Agassiz, [L.] (1850). [Remarks on the little bodies seen on *Hydra*.] Proc. Boston Soc. Nat. Hist. 3: 354–55.

Brouardel, J. (1936). 'Phénomènes nucléaires de la conjugaison chez *Trichodina patellae* Cuénot.' C.R. Acad. Sci., Paris, 203: 818.

Brouardel, J. (1941). 'Variation saisonnière de la densité de population et du nombre de divisions de l'*Urceolaria patellae* (Cuénot) (Infusoires).' Bull. Mus. Océanogr. Monaco, Ser. 2, 13: 314–17.

Brouardel, J. (1946). 'Étude de l'influence de la température sur la durée de division de l'*Urceolaria patellae* Cuénot.' Bull. Inst. Océanogr. Monaco, 43, no. 895: 1–16.

Brouardel, J. (1947). 'Étude du mode d'infestation des patelles par l'*Urceolaria patellae* (Cuénot).' Bull. Mus. Océanogr. Monaco, 44, no. 911: 7 pp.

Caullery, M. & Mésnil, F. (1915). 'Sur *Trichodina patellae* Cuénot (symbiose avec zooxanthelles, structure, division, conjugaison).' C.R. Soc. Biol. Paris, 78: 674–77.

Claparède, E. & Lachmann, J. (1858–60). 'Études sur les infusoires et les rhizopodes.' Extr. Mém. Inst. Nat. Gene. 1: 1–482.

Clark, H. James- (1866). 'The anatomy and physiology of the Vorticellidan parasite (*Trichodina pediculus*, Ehr.) of *Hydra*.' Mem. Boston Soc. Nat. Hist. 1: 114–30.

Diller, W. F. (1928). 'Binary fission and endomixis in the *Trichodina* from tadpoles (Protozoa, Ciliata).' J. Morph. 46: 521–61.

Fantham, H. B. (1930). 'Some parasitic Protozoa found in South Africa, XIII.' S. Afr. J. Sci. 27: 376–90.

Fauré-Frémiet, E. (1943). 'Étude biométrique de quelques Trichodines.' Bull. Soc. Zool. Fr. 58: 158–69.

Fulton, J. F. (1923). '*Trichodina pediculus* and a new closely related species.' Proc. Boston Soc. Nat. Hist. 37: 1–29.

Gray, E. (1948). 'Ciliate protozoan fauna of soil and inland waters.' Nature, Lond., 161: 854.

Harding, J. P. (1937*a*). 'Quantitative studies on the ciliate *Glaucoma*. I. The regulation of the size and the fission rate by the bacterial food supply.' J. Exp. Biol. 14: 422–30.

Harding, J. P. (1937*b*). 'Quantitative studies on the ciliate *Glaucoma*. II. The effects of starvation.' J. Exp. Biol. 14: 431–39.

Hirshfield, H. (1949). 'The morphology of *Urceolaria karyolobia*, sp.nov., *Trichodina tegula*, sp.nov. and *Scyphidia ubiquita*, sp.nov., three new ciliates from southern California limpets and turbans.' J. Morph. 85: 1–33.

Kelser, A. (1921). 'Die sessilen peritrichen Infusorien und Suctorien von Basel und Umgebung.' Rev. Suisse Zool. 28: 221–341.

Komárek, J. (1926). 'Ist die heutige *Polycelis nigra* wirklich nur eine Art?' Zool. Anz. 70: 70–4.

Lender, T. (1936). 'Sur *Polycelia* [*Polycelis*] *nigra* (Ehrbg.) et *Polycelis tenuis* (Ijima) Turbellariés, Triclades.' Arch. Zool. Exp. Gén. Notes et Rev. 78: 49–56.

MacLennan, R. F. (1939). 'The morphology and locomotor activities of *Cyclochaeta domerguei* Wallengren (Protozoa).' J. Morph. 65: 241–56.

Moran, P. A. P. (1949). 'The statistical analysis of the sunspot and lynx cycles.' J. Anim. Ecol. 18: 115–16.

Mueller, J. F. (1932). '*Trichodina renicola* (Mueller, 1931), a ciliate parasite of the urinary tract of *Esox niger*.' Roosevelt Wild Life Ann. 3: 139–54.

Mueller, J. F. (1937). 'Some species of *Trichodina* (Ciliata) from freshwater fishes.' Trans. Amer. Micr. Soc. 56: 177–84.

Mueller, J. F. (1938). 'A new species of *Trichodina* (Ciliata) from the urinary tract of the Muskalonge, with a repartition of the genus.' J. Parasit. 24: 251–8.

Padnos, M. & Nigrelli, R. F. (1942). '*Trichodina spheroidesi* and *Trichodina halli* spp.nov. parasitic on the gills and skin of marine fishes, with special refer-

ence to the life-history of *T. spheroidesi*.' Zoologica, N.Y. 27: 65–72.

Pearl, R. (**1906**). 'Variation in *Chilomonas* under favourable and unfavourable conditions.' Biometrika, 5: 53–72.

Peshkowsky, L. (**1923**). 'Biological and structural features of *Trichodina*.' Arch. Russes. Protist. 2: 249–79. (In Russian with English summary.)

Reynoldson, T. B. (**1947**). 'Urceolarian epizoites of flatworms.' Nature, Lond., 160: 265–6.

Reynoldson, T. B. (**1948**). 'British species of *Polycelis* (Platyhelminthes).' Nature, Lond., 162: 620.

Sekera, E. (**1927**). 'Zur Frage über die *Polycelis*-Arten.' Zool. Anz. 72: 91–8.

Taylor, C. B. (**1940**). 'Bacteriology of fresh water. I. Distribution of bacteria in English lakes.' J. Hyg., Camb., 40: 616–40.

Thorpe, W. H. (**1945**). 'The evolutionary significance of habitat selection.' J. Anim. Ecol. 14: 67–70.

Wallengren, H. (**1897***a*). 'Zur Kenntnis der Gattung *Trichodina* Ehrbg.' Biol. Zbl. 17: 55–65.

Wallengren, H. (**1897***b*). 'Studier öfrer ciliata Infusorier. III. Bidrag till Kannedomen om Fam. *Urceolarina* Stein.' Acta Univ. Lund. 33, pt. 2, no. 8: 48 pp.

Wang, C. C. (**1928**). 'Ecological studies of the seasonal distribution of Protozoa in a fresh-water pond.' J. Morph. 46: 431–78.

Whitehead, H. (**1915**). '[On an epizoic infusorien, *Trichodina steinii* C. & L.; found on Turbellaria.]' J. Quekett Micr. Cl. Ser. 2, 12: 545.

THE STABLE WINTER POPULATION STRUCTURE IN SPECIES OF *MYRMICA*

By M. V. BRIAN
Zoology Department, Glasgow University

1. INTRODUCTION

A detailed study was made of a small colony of *Myrmica laevinodis* Nylander in an observation nest under as nearly as possible natural climatic conditions, but with ample food supply. After each season's activity (growth of larvae, oviposition, metamorphosis, death and replacement of workers), the colony settled down to a definite age composition having quantitative as well as qualitative characteristics. This structure persisted through the winter, and there was no movement of ant material from one stage of ontogeny to another, a condition appropriately described as stable. Examination of colonies of the closely allied *Myrmica rubra* L. collected from the field, confirmed this.

The observation colony was kept in a modified Janet plaster nest, and had access to cultures of *Drosophila funebris* Fab. and other flies as well as candy. Frequent censuses and weighings were performed at intervals appropriate to the rate of change —1 week in summer—1 month in winter. Anaesthetics were avoided, but great care was taken to reduce disturbance, by delicate manipulation early in the day.

2. QUALITATIVE CHARACTERS

Most if not all ants of the genus *Myrmica* hibernate with larvae in their third (final) instar (see also Eidmann, 1943). This is a stage in which considerable growth may occur: during the active season larvae range in length from 1 to about 4 mm., and have a correspondingly large range in weight—from 0·2 to about 3·5 mg. Even in winter a considerable variation in larval size is shown, from the smallest, about 1 mm., up to a limit between 3 and 3·5 mm.—a size beyond which, in normal growth prepupation is inevitable even during starvation.

In the *laevinodis* colony, prepupation * stopped in August (in three consecutive years), the largest larvae failing to transform at temperatures adequate earlier on. After this, until October, many eggs hatched, and the larvae, passing through the first and second instars, entered the third instar. It was these late entries that accounted for most of the smaller hibernating larvae. The average weight of larvae continued to rise until mid-October† after which it began to fall, giving a convenient point from which to date hibernation. In this way, until larval growth was resumed in April, 6 months elapsed, and active and inactive periods divided the year equally. In 1945 the average weight fell from 1·80 mg. on 14 October to 1·31 mg. on 2 December, and in 1946 it fell from 1·44 mg. on 29 September to 1·15 mg. on 8 December. This fall in weight was due to dehydration, a change commonly preceding hibernation in insects. There results a considerable alteration in larval form: the head sinks into the prothorax which becomes flexed ventrally leaving the mesothorax foremost. The abdomen develops an elliptical cross-section (with the short axis dorso-ventral) and has lateral flanges. This contracted, wrinkled appearance contrasts strikingly with the turgid, rotund glistening form of an active larva. No fluids are present in the body cavity which, after sectioning, can be seen to contain only a solid residue, closely packed between fat-body cells. Quite often, though not universally, a drop of orange-coloured oil (about 0·5–0·7 mm. in diameter in large animals) may be found in the mid-gut, within the peritrophic membranes. This is an unusual way of storing fat in insects, but of course few have a septum between mid- and hind-gut. Fat is also stored in the fat-body.

After dehydration, there was little further change in weight during the winter; thus 48 larvae in the *laevinodis* colony weighed 62·9 mg. on 2 December 1945, and 62·3 mg. on 24 March 1946, a loss of only 0·6 mg. Experiment with this colony was not desirable, but it is highly probable that by this time larvae were once more capable of growth and prepupation and merely awaited warmer weather. Larvae of *rubra* collected from the field were not able to resume growth at 20° C. until November, indicating a dormant period of only a few months, but long enough to carry the colony into cool winter weather.

* 'Prepupation' is used instead of 'pupation' because the prepupa is a very conspicuous stage in ant ontogeny. 'Metamorphosis' is reserved for the actual transformation which takes place within these stages.

† Details of the active season will be presented separately.

3. QUANTITATIVE CHARACTERS

(*a*) *A single colony in time*

Mortality in the observation nest was at its lowest in winter: it was in summer that the older workers died, and that the large mortalities associated with ontogeny* occurred. From 28 October 1944 to March 1945 only one larva died: from 21 October 1945 to 24 March 1946 only one worker died: and from 27 October 1946 to 14 March 1947, three workers and three larvae died. In a natural environment disturbance by voles, mice, shrews, and moles is probably appreciable as they seem to have a predilection for burrowing under logs and stones, below which the ants are often found hibernating—principally because these places are especially warm in summer. Possibly some of these small mammals may eat ants during the winter-time. The composition of the population in three successive winters is given in Tables 1 and 2.

(No workers present in the third winter were also present in the first: details of worker survival will be given elsewhere.)

(*b*) *Winter censuses of natural colonies*

M. laevinodis was not present in the area to which the author moved in 1947, and so in the winter of 1947–8, twelve colonies of the closely related *M. rubra* L. var. *macrogyna* Brian & Brian (1949) were collected from a single habitat type in the west of Scotland, just north of the Clyde (National Grid Reference 26/323804). In winter, workers and brood are tightly packed in galleries in the soil extending from a few inches below the surface to about a foot; the surface galleries are vacated by the ants and occupied by non-hibernating soil fauna: slugs, isopods, chilopods, diplopods, Araneida, Collembola, staphylinids, etc. Careful excavation allows all the ants to be collected, free from soil, with a

Table 1. *Numbers and weights (mg.) of workers and larvae in the* laevinodis *observation colony*

	Workers			Larvae		
Winter	Number	Total weight	Average weight	Number	Total weight	Average weight
1944–5	18	47·8	2·66	26	32·2	1·24
1945–6	32	75·0	2·34	48	62·9	1·31
1946–7	49	110·0	2·25	73	84·0	1·15

Table 2. *Ratios and larval size distribution in the* laevinodis *colony*

	Ratios workers/larvae		Size distribution of larvae (mm.)				
Winter	By numbers	By weights	1·0–	1·5–	2·0–	2·5–	3·0–
1944–5	0·69	1·48	9	5	7	5	0
1945–6	0·67	1·19	16	10	7	15	0
1946–7	0·67	1·31	24	22	14	12	1

The total population (P) grew according to the equation $P = 5\ (t+2)^2$ for $t = 1$, 2 and 3 years, which describes a curve bending upwards increasingly rapidly. Of this, two-fifths were workers and three-fifths larvae in each winter—a remarkably constant configuration. The equation relating numbers of larvae (N) to numbers of workers (M) is thus $N = 1{\cdot}5M$, describing a straight line passing through the origin. The ratios of weight are almost as constant as the number ratios, and are satisfactorily described by the equation $L = 0{\cdot}76\,W$ (where L = the total weight of larvae, and W = the total weight of workers)—which also depicts a straight line passing through the origin.

In all years, a full range of larval size was present. The average weight of workers declined slightly.

* 'Ontogeny' is used rather than 'development' which is reserved for use when the whole colony is referred to.

sucking tube of ordinary design. The habitat chosen, was very favourable to this species of *Myrmica*—felled mixed deciduous and coniferous woodland after 10 years of subseral growth. This had resulted in a herb layer consisting mainly of *Agrostis tenuis* and its associated plants, *Potentilla erecta* and *Galium saxatile* interspersed with thickets of *Rubus* sp. and *Betula pubescens* (the latter up to 5 ft. high). Many of the nests were in the old tree stumps, now soft from decay and easily excavated both by the ants and the investigator.

The colonies were sorted into workers and larvae, counted and weighed, and the larvae were measured in a resting position. The results obtained are shown in Tables 3 and 4.

The actual numbers of individuals in the colonies ranged considerably about the averages, 1216 workers and 1378 larvae. No doubt colonies exist

Table 3. *Numbers and weights in natural colonies of* Myrmica rubra *var.* macrogyna

Date of collection	Workers: Number in colony	Workers: Total weight (g.)	Workers: Average weight (mg.)	Larvae: Number in colony	Larvae: Total weight (g.)	Larvae: Average weight (mg.)
2 Jan.	305	0·654	2·14	215	0·173	0·802
26 Dec.	517	1·100	2·12	1100	0·376	0·342
23 Dec.	835	2·115	2·53	1066	0·640	0·602
23 Dec.	850	2·754	3·24	947	0·850	0·898
21 Dec.	1000	2·740	2·74	1064	0·875	0·822
29 Dec.	1230	3·410	2·78	1200	0·830	0·692
26 Dec.	1290	2·790	2·16	1500	0·648	0·432
5 Jan.	1305	3·240	2·48	1132	0·679	0·600
2 Jan.	1320	3·750	2·84	1888	1·320	0·702
14 Dec.	1431	4·765	3·33	1934	1·266	0·655
29 Dec.	1650	3·715	2·26	2300	0·718	0·312
19 Dec.	2855	7·737	2·71	2187	2·467	1·128
Average	1216	3·23	2·66	1378	0·904	0·656

Table 4. *Ratios workers/larvae and size distributions of larvae, in natural colonies of* Myrmica rubra *var.* macrogyna

Number of colony	Ratios workers/larvae: By numbers	Ratios workers/larvae: By weights	Size distribution of larvae (mm.): 1·0–	1·5–	2·0–	2·5–	3·0–
1	1·42	3·78	16	44	39	1	—
12	1·32	3·14	20	22	32	25	1
8	1·15	4·77	29	48	14	4	5
6	1·03	4·11	14	56	18	12	—
5	0·94	3·13	16	51	12	18	3
4	0·90	3·24	5	58	25	9	3
7	0·86	4·31	31	59	10	—	—
3	0·79	3·30	14	59	18	9	—
10	0·74	3·76	25	38	30	6	1
11	0·72	5·17	58	35	7	—	—
9	0·70	2·84	31	34	15	20	—
2	0·47	2·93	28	67	5	—	—
Ratios of totals	0·882	3·58	—	—	—	—	—

in all stages of development from single queens, but not necessarily in habitats that have been inhabited by ants for some years, as this had. Three thousand workers may perhaps be regarded tentatively as lying near the maximum for this species under favourable conditions.

The ratios (numbers) range from 0·47 to 1·42, there being sometimes more, sometimes less larvae than workers, but the ratio of totals lies near to unity. This has little discernible effect on larval size, the range of which is similar to that in the *laevinodis* observation colony.

Numbers of workers and larvae show a good correlation ($r = 0{\cdot}814$; $P = 0{\cdot}01 - 0{\cdot}001$) but it is of exceptional interest to note that an even closer relation connects the *weights* of workers and larvae. In this case the correlation coefficient has the value 0·952 ($P < 0{\cdot}001$), and the regression equation is:

$$L = 0{\cdot}308\,W - 0{\cdot}091, \qquad (1)$$

where, as before, L = the weight of larvae, and W = the weight of workers, both in grams. The standard error of the regression coefficient is 0·0312 g. larvae per gram workers.

This closer relation, particularly as it draws the largest colony (number 12) into line, suggests that a curve might be a more appropriate description of the numbers relationship. In fact, a second degree polynomial:

$$N = -176{\cdot}3 + 1{\cdot}770\,M - 0{\cdot}0003212\,M^2 \qquad (2)$$

(N = number of larvae, M = number of workers) gives a better fit than a straight line, but the reduction in sums of squares of deviations which follows

is not quite sufficient to settle whether the improvement is due to chance or not ($P = 0{\cdot}05 - 0{\cdot}1$). One additional merit of the curve which is worth consideration is that on extrapolation it passes nearer the origin than the line, resembling in this respect the linear weight regression. Unfortunately, the large colonies needed to settle this point are rare and exceedingly difficult to find in winter.

By substituting $L = Nl$ and $W = Mw$, in equation (1) (l = average weight of larvae, w = average weight of workers), it becomes:

$$Nl = 0{\cdot}308\, Mw - 0{\cdot}091,$$

$$l = 0{\cdot}308\, Mw/N - 0{\cdot}091/N,$$

or, writing $R = M/N$, the ratio of numbers of workers to numbers of larvae, and neglecting the second term which, for normal values of N is negligible, the following equation results:

$$l = 0{\cdot}308\, Rw \text{ approximately.}$$

This means, of course, that for a given worker type (average weight = w g.) the average weight of larvae hibernating is proportional to the worker/larva ratio (numbers): or, the more attendants a larva has, the greater the weight it may expect to attain by winter. Evidently the larvae compete for worker attention (their food supply) and the nursing and foraging power of the workers is satisfactorily expressed on any particular occasion by their total weight. Extra-colonial factors such as food supply and temperature as affected by geographical region, season, and habitat, will govern this 'nursing and foraging factor', and different regression coefficients may be expected from colonies collected in different places at different times.

The curved form of the numbers relationship might descend (second-degree polynomial) or approach an asymptote (modified exponential), but in either case its implications are significant: for, in large colonies, the ratio workers/larvae will tend to be high and will bring about an increase in larval size. This improvement in nutrition of the individual may be an important factor in the production of sexual forms, which, in this and other species of ants (Goetsch, 1939) are known to be produced only by large and 'mature' colonies. The primary cause of under-production of larvae must lie with factors governing oviposition; but, whereas it is easy to visualize this as the consequence of the queen reaching her maximum (provided survival of workers is adequate) or declining with age, the fact that worker oviposition is considerable in this species adds many complications.

(*c*) *Comparison of results*

If it is permissible to regard these *rubra* regressions as describing the trend of an average colony as it grows in size (and this is reasonable if environmental conditions are moderately stable), the results for the two methods (and species) agree in pointing to the existence of a quantitative regulation of population composition. They differ in a number of details. The *laevinodis* colony had a comparatively high proportion of larvae, and was able to bring them to a large size (only *rubra* 12 approached their average weight). In *rubra* 9, with a comparable proportion of larvae, the average weight was much lower. These may be species differences, but it is more likely a result of the substitution of human for ant foraging in the captive colony.

Owing to the differences in scale, it is not profitable to make a detailed comparison of the regressions. As regards the numbers relationship, the linearity of *laevinodis* is not incompatible with the curvilinearity in *rubra*, for, when numbers are small, as in *laevinodis*, the second-degree polynomial is practically linear. It may be noted that the slopes are much the same (regression coefficients 1·5 and 1·77). The perfection of linearity in the *laevinodis* numbers relationship leaves little room for improvement in the weights relationship (the former perhaps a result of the uniformity of the non-climatic culture conditions), but the observed discrepancies fall well within the variation expected on a basis of the *rubra* results. The slopes of the weight lines are different (regression coefficients 0·76 and 0·31) expressing the fact already mentioned that the proportion of total population weight due to larvae was greater in *laevinodis*.

The regulatory mechanisms involved in these processes have been studied experimentally, and will be reported subsequently.

4. SUMMARY

Colonies of *Myrmica laevinodis* Nyl. and *M. rubra* L. have a characteristic composition in winter. In an observation colony of *laevinodis* in normal climatic but ample trophic conditions the ratio of workers to larvae was very constant for three successive winters (by number and weight).

Analysis of *rubra* colonies collected from the field in winter gave a good linear regression of larval weight on worker weight, passing through the origin (proportionality). The relation between the numbers of larvae and workers was either subject to more variation (assuming linearity of regression) or failed to achieve linear expectation in large colonies (curvilinear regression). The consequences of this under-production in large colonies, since the average weight was approximately proportional to the worker/larva ratio (numbers) was a higher average weight of larvae. The dominating weight relationship

implies competition between larvae in their 'trophic field', and the results are similar to those usually associated with such in other insects although these do their own foraging and mastication.

REFERENCES

Brian, M. V. & Brian, A. D. (1949). 'Observations on the taxonomy of the ants *Myrmica rubra* L. and *M. laevinodis* Nylander. (Hymenoptera: Formicidae.)' Trans. R. Ent. Soc. Lond. 100: 393–409.

Eidmann, H. (1943). 'Die Ueberwinterung der Ameisen.' Z. Morph. Ökol. Tiere, 39: 217–75.

Goetsch, W. (1939). 'Die Staaten argentinischer Blattschneider-Ameisen.' Zoologica, Stuttgart, 96: 1–105.

ECOLOGY OF FRESH-WATER MOLLUSCA IN THE ENGLISH LAKE DISTRICT

By T. T. MACAN

Freshwater Biological Association, Ferry House, Ambleside, Westmorland

(With 5 Figures in the Text)

CONTENTS

	PAGE
A. Introduction	124
(*a*) Previous work	124
(*b*) Scope of the present work	125
(*c*) Acknowledgements	126
(*d*) General description of the area and definition of some terms	126
(*e*) Arrangement and presentation of the work	126
B. Gastropods	126
1. Windermere	126
(*a*) Description	126
(*b*) Method of collecting and results	126
(*c*) *Hydrobia jenkinsi*	127
2. Other lakes	129
(*a*) Description	129
(*b*) Method of collecting and results	129
3. Tarns and pools	130
(*a*) Physical and botanical features	130
(*b*) Chemical features	130
(*c*) History and method of collecting	135
(*d*) Results	135
4. The fresh-water limpets	142
C. Lamellibranchs	142
D. Summary	144
References	146

A. INTRODUCTION

(*a*) *Previous work*

Boycott (1936) has summarized what is known about the ecology of fresh-water molluscs in Britain. He defines a 'good' mollusc habitat as one which is large, has a slow flow of clean water, is warm, has a fair but not excessive growth of rooted plants, and contains hard water. Such a place will contain many species, and Boycott believes that these conditions are 'good' for nearly every British species; only a few are confined to peculiar and restricted habitats. As conditions depart from the optimum, some species disappear, different ones according to which feature of the environment deteriorates.

A calcium concentration of about 20 mg./l. is a critical figure below which a number of species, which may be referred to as calciphiles, seldom or never occur. Others can tolerate lower concentrations, but they may be found also where the calcium exceeds this value, and Boycott is doubtful if there is any species which can truly be called calcifuge.

Competition may be a factor of importance, particularly in small ponds. Further, there is always also the question of how far the fauna of such places is due to chance. Boycott found that many species of snail were surprisingly often transported to ponds unconnected with any other piece of water (though he did not elucidate the nature of the vehicle), but that a few possessed little ability to traverse land barriers.

Hubendick (1947), in a detailed study of the subject in Sweden, reaches substantially the same conclusions as Boycott. He arranges his stations in various categories, some of them overlapping, and concludes that a rich mollusc fauna is, on the average, associated with deciduous forest, cultivated land, clay soils, calcareous areas, abundant vegetation, and eutrophic conditions; a poor one with pine forests, areas deficient in calcium and clay, in waters with little organic matter or where decomposition of organic matter is retarded, in places lacking vegetation, and in dystrophic water. Alsterberg (1930), also working in Sweden, was interested primarily in the depth distribution of fresh-water snails. He found that most are confined to shallow water where there is sufficient light for vegetation, and few occur in the deeper parts of deep lakes. Unexpectedly these are not gill-breathers, but lung-breathers, usually *Limnaea* and occasionally *Planorbis*. Both must have air at summer temperatures in shallow water, but at low temperatures such as obtain in winter, or throughout the year in the hypolimnion of stratified lakes, they can obtain all the oxygen they require from solution. After extensive biological investigations, Alsterberg concludes that the more catholic feeding habits of

Limnaea enable it to extend its range to depths uninhabited by other genera.

Lang (1931) transferred adults and eggs of *L. stagnalis* and *L. pereger* to fishponds where neither species occurred. The adults survived and apparently throve, but eggs did not develop. He mentions three factors that might have been adverse, but offers no experimental analysis of their effects. It is generally true that the study of the ecology of fresh-water Mollusca has reached a stage where distribution in the field has been correlated with certain attributes of the habitat, but not the stage of experimental investigation of the nature of this correlation.

Frömming (1936, 1938), collecting in northern Europe, concludes that the poor fauna associated with acid peaty water is due to poor food supply and is not related directly to any chemical factor; his argument is strongly attacked by Hubendick (1947). The latter shows that the thickness of the shell of *L. pereger* varies according to the amount of calcium available, but there is no experimental evidence that any species of snail is excluded from any habitat because there is not enough calcium to build a shell (Robertson, 1941). It is pertinent that other groups, without a calcareous shell or skeleton, have calciphile and non-calciphile species.

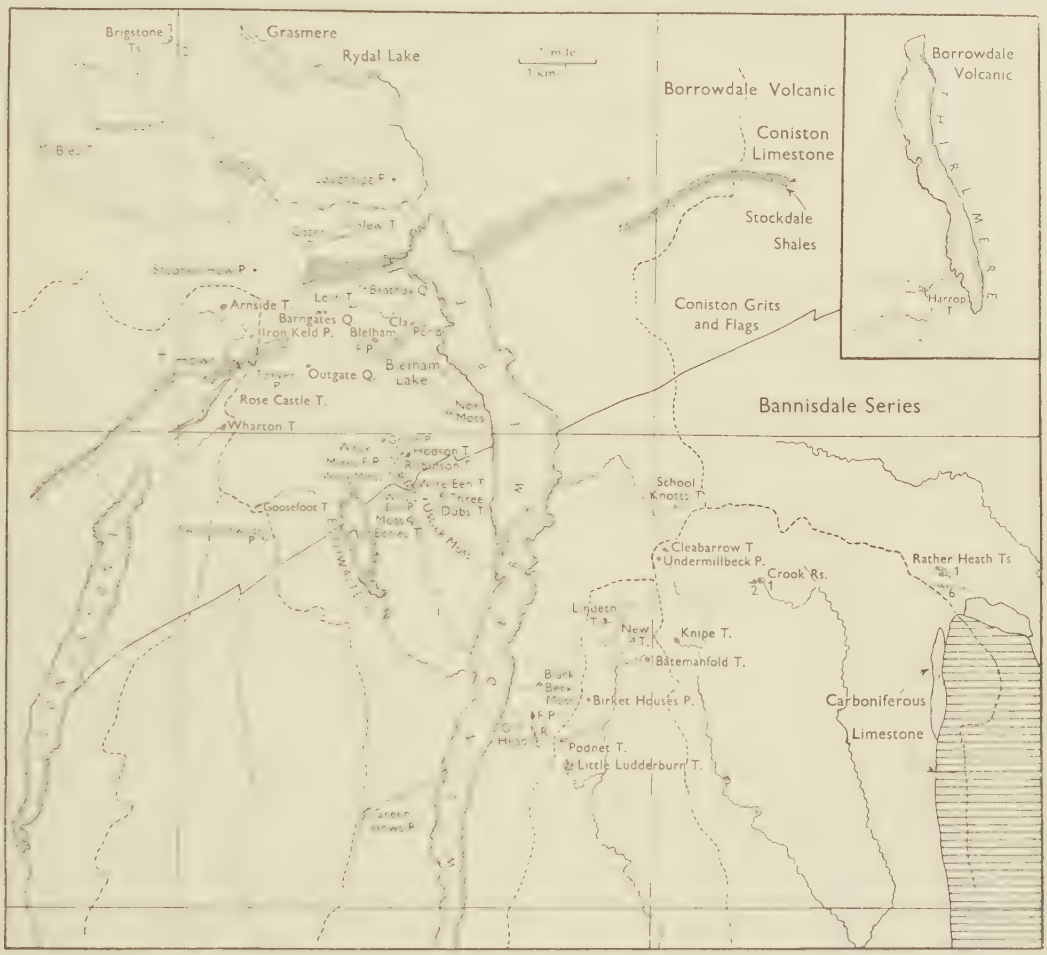


Fig. 1. The tarns and pools and some of the lakes studied; solid geology; and drainage areas. (T. = tarn; P. = pool.)

(*b*) *Scope of the present work*

Much of Boycott's review is based on casual collections from widely separated localities, the present work on detailed study of a large number of water-bodies in a small, geologically uniform area. An attempt is made to correlate each species found with physical and chemical features of its habitat; the experimental analysis stage has not been reached.

(*c*) *Acknowledgements*

I wish to express my gratitude to three experts who have done much of the identification and who have uncomplainingly worked through large collections of commonplace material. The late Prof. A. E. Boycott, F.R.S., and then Mr G. I. Crawford named the earlier collections of gastropods, and the late Mr C. Oldham the lamellibranchs. Later collections of gastropods have been identified by the author.

An essential part of the study has been the chemical analyses carried out by Mr F. J. Mackereth and Dr C. H. Mortimer, and the botanical studies, in which I have received help from Dr J. W. G. Lund; I record with pleasure my indebtedness to these colleagues.

(*d*) *General description of the area and definition of some terms*

Lake District rocks are hard and deficient in calcium, and most of the area is unproductive moorland. The fellsides are utilized as rough sheep grazings and the valley bottoms are tilled.

It is convenient to recognize three types of water-body in the Lake District: lakes, tarns, and pools. Lakes lie in the main valleys and receive water from large drainage areas; all are glacial in origin. Tarns lie in side valleys and have small drainage areas. A useful, but not absolute, distinction is that the common emergent plant is *Phragmites communis* in lakes and *Carex rostrata* in tarns. These criteria, it must be pointed out, cut across the distinction recognized by the Ordnance Survey and local inhabitants, and waters such as Blelham 'Tarn' become lakes. Some tarns were formed during the Ice Age, others are recent and artificial. Pools are usually smaller and shallower than tarns, but the most satisfactory distinction is that pools have no perennial outflow, whereas tarns have, except perhaps after an exceptionally long dry spell. In one or two instances where there has been some doubt, the showing or otherwise of an outflow on the 6 in. to 1 mile Ordnance Survey maps has been accepted as a ruling.

It is convenient to refer to high tarns or pools and low tarns or pools, using the 1500 ft. contour (457 m.), which appears to be significant in the distribution of other groups (Macan, 1938, 1940), to separate them.

(*e*) *Arrangement and presentation of the work*

Mollusc collections made during the course of other work (Macan, 1938) from 1935 onwards suggested that further study of the gastropods would prove worthwhile, and this has been done; the lamellibranchs appeared to be less interesting ecologically and further collections were not carried out. Gastropods and lamellibranchs are, therefore, treated in separate sections in the following pages. Further, among the gastropods, *Ancylus* and *Ancylastrum* are treated separately because, being species which are not usually taken in collections made with a pond-net, they have been rather neglected.

The gastropod population of Windermere is described first, separately from that of the other lakes, as it has been investigated more thoroughly; Windermere and the other lakes are then compared (p. 129). Finally, the snail population of tarns and pools is discussed (p. 130), this being the part of the work to which most time has been given.

B. GASTROPODS

1. Windermere

(*a*) *Description*

The north basin of Windermere, the only one studied, is roughly half a mile (800 m.) wide, and 5 miles (8 km.) long; its greatest depth is 219 ft. (67 m.). About 30% of the drainage area is cultivated and there is a small town, Ambleside, on one of the main inflows.

Most of the lake bottom is stony in shallow water, with little vegetation except investing algae, some *Littorella uniflora*, and an occasional tuft of *Myriophyllum* sp. On sandy bottoms *Littorella* forms a continuous sward. There are about twelve reed-beds, all of small size, in bays sheltered from excessive wave action. The most exposed have a sandy bottom with a low percentage of organic matter in the soil and a flora of *Phragmites* and *Littorella*, the least exposed a muddy bottom with a high percentage of organic matter (figures in Macan, 1938) and a more varied flora which may include *Carex* spp. and *Equisetum fluviatile* with *Scirpus lacustris* in the deeper water.

A rich submerged vegetation, including several species of *Potamogeton* and *Elodea canadensis*, is found between depths of 2 and 5 m.

(*b*) *Method of collecting and results*

Molluscs were collected by means of a pond-net in shallow water and a small trawl in deeper water. A few quantitative samples were obtained in shallow water with a grab covering an area of 1 sq. ft.

The 57 stations worked can be divided into four different categories: (1) on the exposed stony shores; (2) in reed-beds with *Phragmites* and *Littorella* on a sandy bottom. The percentage of organic matter ranged between 3·0 and 11·0% except at one station where an unexpectedly high figure of 31·0% was obtained; (3) in reed-beds with a more varied flora

and a muddy bottom. The percentage of organic matter ranged from 15·0 to 52·0%; (4) in the submerged vegetation in deeper water.

Since a station is not definable precisely in terms of area covered or energy expended, total numbers caught are not comparable and a more reliable picture is given by a study of presence and absence. Table 1 shows the number of stations at which each species was recorded. There are in the four categories 18, 12, 19 and 8 stations, totals which are not large enough to warrant conversion of the results to per cent, but which can be brought to 12 or very nearly 12 by multiplication by a simple factor. This step, which makes all the catch figures almost exactly comparable, has been taken in Table 1.

The first six species are all common and widely distributed in the lake. *Limnaea pereger* is the most widespread, though the total number taken is less than that of some of the others. The χ^2 test applied to *Planorbis carinatus* and *P. albus* reveals nothing significant, but, since only four out of a total of 306 specimens of *P. carinatus* were taken in the submerged vegetation, it obviously is a species of the shallow water. The next three of the six common species all occur more often in the submerged vegetation than at other stations. The χ^2 test shows that the results for *P. contortus* are just significant and those for *Valvata piscinalis* and *Physa fontinalis* highly significant. Many more of each of the three were caught in submerged vegetation than elsewhere. Humphries (1936), investigating the fauna of the deeper parts of Windermere, found that at a depth of 3 m. these three were the only frequent species. *Limnaea pereger*, the only other snail, was rare. At greater depths there were but two species, *Valvata piscinalis* which extended to a depth of 9 m. and *Limnaea pereger* which, though scarce, ranged to the deepest parts of the lake.

The less common species remain to be discussed (Table 1). *Limnaea palustris* was found on all types of substratum, though never far from the margin of the lake, and its presences and absences in Windermere, as elsewhere, were not easy to account for. *Planorbis complanatus*, *P. spirorbis* and *Myxas glutinosa* were taken in small numbers at few places. The last species, *Hydrobia jenkinsi*, merits more detailed treatment.

First, however, some notice may be taken of the numbers of all species per unit area. Six grab hauls on *Littorella*, or *Phragmites* with *Littorella*, caught an average of 3·3 snails, the highest total being 6 and the lowest 1. But, when vegetation offering more cover was sampled, much higher numbers were obtained; an isolated tuft of *Myriophyllum* yielded 108 snails, and there were 63 in a square foot of *Potamogeton natans*. No quantitative collections from the deep-water vegetation were made.

The figures given by Humphries (1936) and Moon (1934, 1936) are of the same order. It is, incidentally, not clear what Moon means by *Planorbis crista* in his table IX (1934), as this name does not appear in the complete fauna list in the appendix.

(*c*) Hydrobia jenkinsi

A survey of the shallow water of the north basin of Windermere in 1936 revealed the presence of this species at six places, all close together in or near Whitecross Bay, on the north-east shore of the lake. At station 1 a single specimen was taken, at stations 2–4 a few were found, at station 5 there were very large, and at station 6 fair, numbers of *Hydrobia*.

In October 1937 a detailed survey of the south-east corner of Whitecross Bay was carried out with the assistance of Dr Betty Carey, to whom I wish to express my best thanks. The lake here is floored with sand, on which grows a sward of *Littorella uniflora* with some *Lobelia dortmanna*. Along the south shore there is a bed of *Phragmites*. A fair-sized stream enters the south-east corner of the bay.

The gently shelving contours of Whitecross Bay have been interrupted by the activities of a sand-dredger, and in the south-east corner there is a steep-sided chasm 9 m. deep. At the landward end, three pits, each about 3 m. deep, are connected with the chasm and with each other. The chasm itself is too deep for vegetation, but in the pits there is a good growth of *Potamogeton perfoliatus*, *P. alpinus*, *Elodea canadensis*, *Callitriche* sp., *Sparganium minimum*, and a patch of filamentous green alga.

It was within these pits that *Hydrobia* occurred in greatest numbers, and we estimated, after a few hauls with a Petersen grab, that the density was of the order of 1000 per sq. ft. (about 10,000 per sq. m.). *Hydrobia* extended on to the *Littorella* surrounding the pits and into the *Phragmites* bed to the south, but in greatly diminished density, and within 30 yd. at the most from the lip of the pits it was not found at all, except at the apparently isolated stations to which reference has already been made.

The original intention was to repeat this survey after about 5 years, but the war intervened and Whitecross Bay was not revisited until October 1946. Unfortunately in the interim an aircraft assembly factory had been erected on its shores, and a concrete jetty had been built into the middle of the place where *Hydrobia* had been most abundant in 1937. What effect this may have had was impossible to assess, nor, although there was no positive evidence, can pollution of the stream by the workshop built on its bank be ruled out as a possibility. The explanation of the great decrease found must, therefore, remain unknown. *Hydrobia* was not found at all at stations 1–4. At station 5 it was scarce; collections

Table 1. *Number of stations in Windermere at which the various species of mollusc were recorded*

	Actual number of stations	Factor	Corrected number of stations	*Limnaea pereger* (Müll.)	*Planorbis carinatus* Müll.	*P. albus* Müll.	*Valvata piscinalis* (Müll.)	*Planorbis contortus* (L.)	*Physa fontinalis* (L.)	*Limnaea palustris* (Müll.)	*Planorbis complanatus** (L.)	*P. spirorbis* (L.)	*Myxas glutinosa* (Müll.)	*Hydrobia jenkinsi* Smith
Exposed shore	18	$\times\frac{2}{3}$	12	9·2	6·6	7·2	2	3·2	1·2	1·2	.	.	.	0·6
Reed-bed on a sandy bottom	12	$\times 1$	12	8	8	9	4	4	1	1	.	.	.	1
Reed-bed on a muddy bottom	19	$\times\frac{2}{3}$	12·6	8·6	8	4·6	5·2	2	1·2	2	1·2	.	.	.
Submerged vegetation	8	$\times\frac{3}{2}$	12	10·5	4·5	6	12	7·5	7·5	.	3	1·5	1·5	.
Total	57	.	48·6	36·3	27·1	26·8	23·2	16·7	10·9	4·2	4·2	1·5	1·5	1·6

* Referred to as *Planorbis fontanus* Lightfoot by Boycott (1936) who uses the name *Planorbis complanatus* Studer for the species more usually called *Planorbis planorbis* (L.).

Table 2. *Number of stations in each lake at which each species was taken*

Lake	Calcium (mg./l.)	Number of stations	*Limnaea pereger*	*Planorbis albus*	*P. contortus*	*Valvata piscinalis*	*Physa fontinalis*	*Limnaea palustris*	*Planorbis carinatus*	*P. complanatus*	*P. spirorbis*	*Limnaea truncatula*	*Myxas glutinosa*	*Hydrobia jenkinsi*
Ennerdale	2·3	8*	5	.	.	.	.	.	.	.	.	.	.	.
Crummock	3·0	1	1	.	.	.	1	.	.	.	.	.	.	.
Loweswater	4·2	2	2	2	2	.	1	.	.	.	.	.	.	.
Derwentwater	6·6	8	4	3	5	1	.	.	.	.	3	1	.	.
Brotherswater	4·6	3	3	2	1	1	1	.	.	.	.	.	.	.
Ullswater	4·8	17	14	.	1	6	2	2	.	.	.	.	.	.
Bassenthwaite	4·6	5	5	3	1	1†	3	3	.	.	3	2	.	.
Coniston	7·1	4	4	3	2	2	2	1	.	1†	.	.	.	.
Grasmere	6·4	12	4	4	7	2	10	.	.	.	.	.	.	.
Rydal	6·2	11	6	3	5	3	8	2	.	.	.	.	.	.
Windermere	5·0	49	35	27	12	15	5	6	30	2	.	.	.	1
Esthwaite	7·0	8	5	5	4	4	1	1	.	.	.	.	.	.
Blelham	8·9	4	3	3	1	1	3	2	.	1	.	.	.	.

* Five with trawl. † Single specimen. *Valvata cristata* Müll. was found in Esthwaite in 1949 and in Blelham in 1950.

with a plant-grab in the pits, where previously the snail had been so numerous, did not produce any, and only on an isolated plant of *Potamogeton alpinus* in the *Phragmites* bed were a few specimens found. On the other hand, at station 6 numbers appeared to have undergone no diminution.

In June 1948, Mr G. J. Thompson recorded that *Hydrobia jenkinsi* was present in great numbers in a stream which entered the lake about 2 miles south of Whitecross Bay. It had definitely not been there in May 1947 and none had been found in January 1948, but, since conditions had been difficult for collecting, he was not certain about absence on this later date.

In August this stream was examined carefully. For the last mile its course is underground through Windermere town. *Hydrobia* occurred in a stretch of about 1 mile above this, though it was abundant only in a stretch about 300 yd. long near the upper end of this mile. Upstream of the zone of abundance numbers dropped rapidly and none was found in two tributaries. Downstream the drop in numbers was less rapid but, half a mile from the region of great abundance, diligent search was necessary to find a specimen.

There were a few at the mouth of the stream, and they extended southwards along the lake shore for less than 50 yd. Northwards, *Hydrobia* was fairly abundant in the south-east corner of a bay; but it could not be found in a *Phragmites* bed in the north-east corner.

2. Other lakes

(*a*) *Description*

The Lake District lakes can be arranged in a series. At one end is Ennerdale lying in a band of hard rocks which have weathered little; the shores are stony; the drainage area is little cultivated and almost uninhabited; *Nitella opaca* Ag. and *Isoetes lacustris* are the only common plants. At the other end is Esthwaite lying in softer, more weathered rocks; its shores are silted and reed-beds are extensive; the drainage area is well populated and nearly half of it is cultivated; the flora is rich in number and species. In Table 2 the lakes are arranged in order between these two extremes (Pearsall, 1921).

(*b*) *Method of collecting and results*

Except in Ennerdale, where the trawl was used to collect in the deep-water vegetation, all the collections have been made with a pond-net in shallow water. The stations are of unequal value but the total number does give some indication of the amount of time spent at each lake. In Table 2 the number of stations at which each species was found is shown. The shallow-water stations of Windermere are included for comparison. The Windermere list is the longest, probably because more time has been spent collecting in that lake.

There are two outstanding points in the table. The first is the poor fauna in the primitive lakes. Rather thorough investigation of Ennerdale yielded only *Limnaea pereger*. In Crummock Water *Physa fontinalis* occurred as well. It was found near the inflow, the only place where vegetation grows in shallow water; no search was made in deep water. Sewage from the small community at Buttermere village may have had a locally favourable effect just here.

The other point is the abundance in Windermere and absence from all other lakes of *Planorbis carinatus*. Boycott lists it among the calciphiles, that is a species not to be expected in a concentration of less than 20 mg./l. of calcium. He notes, however, that large size of a water-body is an ecological factor which may compensate for a low calcium concentration, and the occurrence of *P. carinatus* in Windermere is an illustration of this. *P. carinatus* had not spread to any other lake by 1940, nor to Blelham by 1948, though both Esthwaite and Blelham are likely to be more suitable than Windermere. Both are connected to Windermere by quite short rivers with extensive sluggish reaches.

The remaining lakes have, in general, a similar snail fauna, though there are certain differences in the relative abundance of the species present. These differences show some correspondence with the geology though it is not possible to say whether this is significant. In Windermere, Esthwaite, Blelham and Coniston, the four lakes on the Bannisdale Slates, the six common species occur in similar proportions. Derwentwater, Loweswater and Bassenthwaite, all on the Skiddaw Slates, are characterized by scarcity of *Valvata piscinalis*, and the last two are further linked by the occurrence of both *Planorbis spirorbis* and *Limnaea truncatula* (Müll.), species recorded from no other lake.

Of the lakes on the Borrowdale Volcanic rocks, Brotherswater has a fauna rather like that of the Bannisdale Slate lakes. Ullswater is the most aberrant of all, and on this account has been searched more thoroughly than any other except Windermere. *Limnaea pereger* was widely distributed and sometimes present in fair numbers; *Valvata piscinalis* was fairly frequent; *Planorbis contortus* was found only at one place, where, however, it was numerous; *Physa fontinalis* was scarce; and *Limnaea palustris* was found in fair numbers on a sward of *Littorella*. *Planorbis albus*, usually one of the most frequently encountered species, was not taken at all—a surprise, for it occurs in Brotherswater 3 miles up the valley. Rydal and Grasmere, which come low in Table 2,

because their volumes are relatively small and the human communities beside them large, differ from all the rest in that *Physa fontinalis* is the species encountered most often. This was so both before and after the war.

3. Tarns and pools

(*a*) *Physical and botanical features*

Nearly all the tarns at high altitudes are of glacial origin. On the lower fells there are, in addition, many man-made fishponds formed by damming valleys. The age of such tarns is important in an investigation of the present kind. Two, Arnside and Rose Castle (Fig. 1), were made in the twenties, and three, Little Ludderburn, New, and Podnet, about 1933. The rest are shown on the 1911–12 edition of the 6 in. to 1 mile maps and therefore were at least 23 years old when the investigations started.

A high natural tarn usually has a rocky or stony bottom except in the deepest water, where there may be a substratum of finer particles. *Isoetes lacustris*, *Nitella opaca*, and *Myriophyllum* spp. occur in the deeper, and *Littorella uniflora* and *Juncus bulbosus* forma *fluitans* in the shallower water. A few have reached a stage where accumulation of plant remains has built up an organic bottom on which there is an extensive growth of *Potamogeton natans*. This ultimately gives place to *Equisetum fluviatile*, *Menyanthes trifoliata*, *Carex rostrata*, and *Sphagnum* spp., and the area becomes a moss.

The botanical history of an artificial tarn is somewhat different, for, when it is created, there is always some soil on the land which is flooded, and this forms a substratum in the new aquatic environment. If the tarn be large, the soil, usually peat, may be eroded from the shallow regions but there is always a fair thickness in the deeper water. *Littorella uniflora*, *Juncus bulbosus* f. *fluitans*, *Apium inundatum*, *Sparganium minimum* and, if the peat has not been eroded, *Lobelia dortmanna* are the common species of the shallow water. The deep-water communities are also richer in species than those of natural tarns, and additional plants recorded are *Callitriche* spp., *Elodea canadensis* and occasionally such species as *Potamogeton obtusifolius* and *P. alpinus*. I wish to thank Mr J. E. Dandy of the British Museum for his kindness in naming these species of *Potamogeton*.

Conditions in the natural tarns are, in general, more austere than in the artificial tarns, and probably this is to be correlated with altitude and temperature acting directly and indirectly. The rate of evolution of natural tarns is obviously extremely slow and measurable in centuries, that of artificial tarns is much faster. There is no accurate information and probably, if there were, it would show great variation from tarn to tarn. During the 10 years of this investigation, most of the tarns have changed little, to judge from sketch-maps made on different occasions, but three have changed greatly. One of these was new when first visited; the other two were heavily overgrown, and deterioration of the dam has evidently speeded up the rate of change.

An artificial tarn with a submerged flora, such as has just been described, fairly soon reaches a stage where extensive areas are covered with *Potamogeton natans* and water-lilies. *Carex rostrata* encroaches from the sides, or sometimes starts in the middle and grows outwards, and, in the last stages of what can possibly be called an aquatic environment, the tarn is overgrown by *Carex* and *Sphagnum*, often apparently floating. Associated plants are *Salix* spp., *Menyanthes trifoliata*, *Hydrocotyle vulgaris* and other typical bog species.

Some of the pools, being recent quarry excavations, tend to have straight sides, a great depth relative to the surface area, and no higher plants. Most are erosion basins in peat-beds. *Sphagnum* spp., *Utricularia* sp., *Juncus bulbosus* f. *fluitans*, *Lobelia dortmanna* and *Potamogeton polygonifolius* are the characteristic plants, with *Carex rostrata* and species of *Sphagnum* coming in at the later stages.

No correlation between any plant and any snail has been found, but the stage of evolution which a tarn has reached does seem to be a factor in snail ecology. The process of evolution already outlined can conveniently be divided into three stages: (1) submerged plant stage, when *Potamogeton natans* and water-lilies, if present at all, occupy less than half the tarn, and *Carex*, if present at all, is confined to small patches (*Littorella* is usually to be found fairly abundantly); (2) floating-leaf stage, when *Potamogeton natans* and/or water-lilies occupy at least half the tarn, but *Carex* is still confined to bays; (3) emergent vegetation stage where the *Carex* beds are large and extensive, and any open water is overgrown with floating-leaved species.

Such changes will obviously affect the physical and chemical conditions. Floating leaves will hinder the mixing of water by wind, and emergent vegetation will tend, by confining through currents to a defined channel, to prevent lateral mixing. There will be increased loss of water at the surface, and the accumulation of plant remains on the bottom will lead to different conditions. But a study of these effects has yet to be made.

(*b*) *Chemical features*

Previous work has established that calcium is a factor in snail ecology, but most of the conclusions are based on a single analysis of each water-body; it seemed to me that some knowledge about fluctuations in calcium concentration might prove important.

First, that concentration may vary in different parts of a heavily overgrown tarn, as postulated in the preceding section, is shown by the results from a place which is shown diagrammatically in Fig. 2. The main flow of water is probably through the zone of *Carex* and *Potamogeton polygonifolius*, where vegetation is least thick. The figure shows also the positions of the stations where samples were taken during the long dry spell in August 1947, and Table 3 flow water. Such a range has been assumed to be exceptional, for Tarn Hows is unique in the present series in receiving drainage from the Coniston Limestone, and the streams with the high values flowed off this formation.

Thirdly and finally there is the variation due to rainfall. Fig. 3 shows the fluctuations in two tarns which have been sampled during the course of a year, not at regular intervals, but whenever the incidence

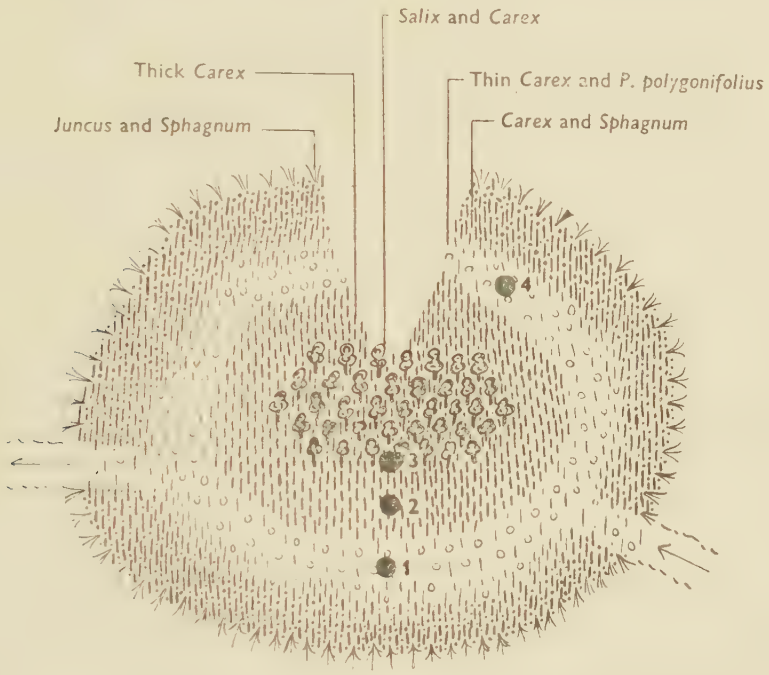


Fig. 2. Diagram of the vegetation in Black Beck Moss and the position of the sampling stations.

Table 3. *Alkalinity and calcium concentration in Black Beck Moss on 26 August* 1947

	Station 1 (south channel)	Station 2 (middle of *Carex*)	Station 3 (edge of island)	Station 4 (north channel)
Alkalinity ($CaCO_3$ equiv.) (p.p.m.)	19·9	20·5	12·1	23·2
Actual calcium (p.p.m.)	8·5	8·8	7·6	10·4

the results of the analysis. The highest calcium concentration is nearly half as much again as the lowest, and the highest alkalinity is nearly double the lowest.

Secondly, calcium concentration may be expected to vary from place to place because the inflowing streams bring in different amounts. Table 4 shows the variation in two tarns. In the second, Tarn Hows, the variation is considerable and great enough to invalidate conclusions based on an analysis of the out- of rainfall made it likely that an analysis would be interesting. Three Dubs Tarn is a typical fishpond with vegetation at stage 1; Blelham Fishpond has reached stage 3, and the size of its drainage area is above the average. Calcium was measured direct by a method evolved by Mr F. J. Mackereth (this method involves precipitation with picrolonic acid, and it is hoped that an account will be published shortly). Alkalinity was ascertained by titration

Table 4. *Actual calcium content of the waters of the inflowing streams of two tarns*

Inflow no. ...	1	2	3	4	5	6	Outflow
Three Dubs (p.p.m.)	6·4	4·4	3·3	5·2	3·3	4·4	3·2
Tarn Hows (p.p.m.)	6·8	26·3	12·2	10·2	3·2	·	4·3

against HCl and expressed as the $CaCO_3$ equivalent. The usual practice is to express the latter in this way, but in Fig. 3 the equivalent of Ca or 'theoretical calcium' (being 40% of the $CaCO_3$ equivalent) has been plotted.

There is a general correlation with rainfall, but much in Fig. 3 remains obscure. Towards the end of an exceptionally long dry spell in August 1947, the values in Blelham Fishpond were high and theoretical calcium exceeded actual calcium for the only time during the period of observation. There was a week of moderate rain in September, and the theoretical calcium fell to a third of its previous value; actual calcium fell at first but by the end of the wet spell it was at its highest value of the year. It then dropped but rose again during a relatively dry October. A day in November with 2½ in. of rain produced a big drop, and theoretical calcium reached a minimum. The next analysis showed a rise, although there had been a week of moderate rain. This rise probably continued throughout a dry December but no sample was collected. Heavy rain in January and February brought the level down again and actual calcium reached its lowest level.

Though the trend is similar, the figures for Three Dubs Tarn show differences in detail. Fluctuations are smaller and theoretical is always less than actual calcium. The values reached in August 1947 are not particularly high, and the actual calcium rose throughout October to reach a maximum on 11 November, the sample being taken on one of the wettest days of the year though before most of the rain had fallen. The theoretical calcium reached its highest point in August 1948.

Studies of the effect of rainfall on the drainage area will be necessary before these results can be explained completely.

The results from all the tarns are shown in Table 5; the second column gives sizes in units of 1000 sq. yd., and the rest chemical data based on samples from the outflow. The analyses were made towards the ends of periods of uniform weather, a long wet spell in January and February 1948, a long dry spell in January 1947, a short dry spell in August 1948, and a long dry spell in August 1947. No series, except the first, is complete, since each time some tarns had to be omitted because they had been drained or manured, and in August 1948 rain started before the round was complete.

Calcium is low in all the tarns, on Boycott's reckoning. The lowest value is usually found in the wet spell in winter, and the highest in the dry spell in summer, the dry spell in winter being intermediate, but there are nine exceptions to this among the tarns, and in one of them, Rather Heath 1, the lowest value was obtained in summer. Unexpectedly, of fourteen samples taken during an exceptionally long fine spell in August 1947 six are lower than in August 1948 when the fine spell was of much shorter duration.

The ratio of lowest to highest calcium value is shown in the last column but one; the lowest and highest have been taken regardless of the season when they occurred, but the results obtained in August 1947 have been omitted, since only a few of the tarns were sampled then. The lowest ratio is 1·1, the highest 2·7, though it would have exceeded 3 had the August 1947 figures been included. The greatest range appears to be associated with advanced development of vegetation, as may be seen in Table 6. Brigstone 1 and 2 have not been included because no summer sample was obtained but, if the two winter samples are compared, the ratio is over 2 in both tarns although they are at stage 1.

Clearly the alkalinity was not all due to $CaCO_3$, but, in the absence of precise knowledge, this convention will serve as well as any. In thirteen tarns the theoretical calcium of the highest reading exceeded the actual calcium, so presumably some element besides calcium was causing the alkalinity. In the other tarns there was more calcium than was to be expected from the alkalinity, and in them part of the calcium was presumably balanced by some radical other than carbonate. When the lowest values are considered, the theoretical, with three exceptions, is found to be less than the actual calcium, and the difference is almost always greater than in dry weather. Whatever causes the alkalinity is apparently more affected by rainfall than the calcium not associated with carbonate. This is shown well in Fig. 3.

The tarns fall into three groups according to whether the lowest alkalinity is:

A, higher than the highest calcium;
B, between the lowest and highest calcium;
C, lower than the lowest calcium.

These letters denoting the categories are shown in the last column of Table 5. Since it is not known what causes the alkalinity, the significance of this classification is obscure, but it seems to be a factor of importance in snail ecology.

The electrical conductivity is found to be associated closely with the calcium concentration.

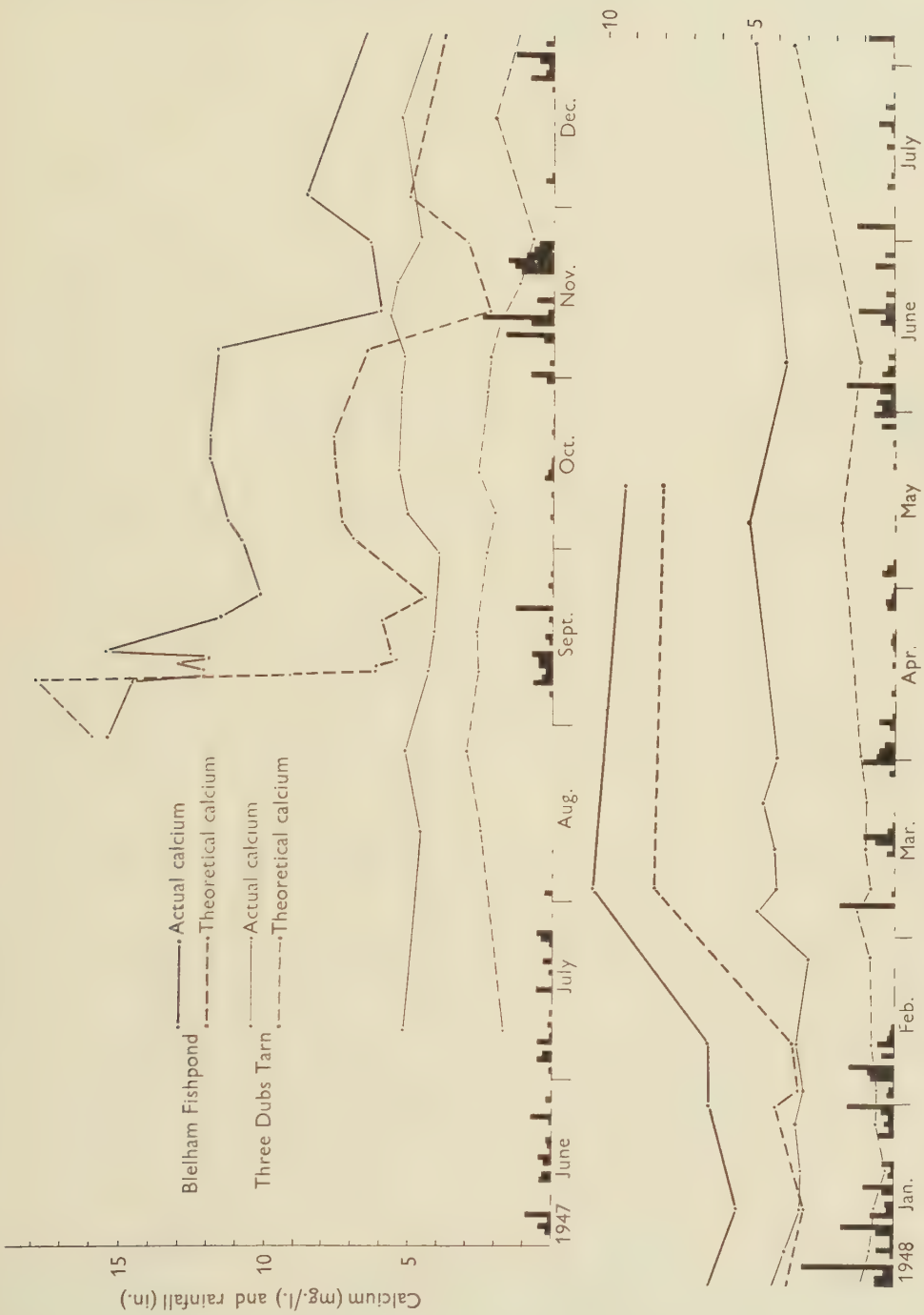


Fig. 3. Rainfall and the fluctuation of calcium and theoretical calcium (i.e. calcium calculated from alkalinity) in Three Dubs Tarn and Blelham Fishpond.

Table 5. *Chemical data for tarns and pools*

	Size (1000 sq.yd.)	Jan./Feb. 1948, wet spell in winter: Actual Ca (mg./l.)	Alk. (mg./l.)	Electrical conductivity K 250 $^{10-6}$	Jan. 1947, dry spell in winter: Ca (mg./l.)	Alk. (mg./l.)	Aug. 1948, short dry spell in summer: Actual Ca (mg./l.)	Alk. (mg./l.)	Electrical conductivity K 250 $^{10\ 6}$	Aug. 1947, long dry spell in summer: Ca (mg./l.)	Alk. (mg./l.)	Botanical stage	Ratio highest: lowest calcium	Lowest alkalinity less lowest calcium
Tarns:														
Rather Heath 6	7·7	16·6	39·9	113	21·0	62·5	29·6	92·3	173	·	·	2	1·8	23·3 A
Rather Heath 1	25·2	15·2	27·6	102	17·8	34·6	14·2	37·4	101	·	·	1	1·3	13·4 A
Rose Castle	5·8	9·6	17·9	81	5·8	14·4	12·9	30·0	95	12·2	34·3	2	2·2	8·6 A
Crook Upper	2·3	9·4	15·6	78	11·0	20·1	15·4	45·6	103	·	·	2	1·6	6·2 A
Cleabarrow	6·6	9·2	16·6	78	10·6	24·0	14·1	37·7	81	·	·	1	1·5	7·4 A
Little Ludderburn	40·0	8·6	15·1	76	16·0	33·5	19·2	58·1	132	26·5	70·6	3	2·2	6·5 B
Crook Lower	9·0	8·0	16·3	71	11·2	30·7	16·4	47·5	120	·	·	3	2·0	8·3 B
Clay Pond	0·7	7·6	8·1	80	10·0	15·0	12·5	26·3	95	·	·	1	1·6	0·5 B
Slew	6·2	7·1	8·9	67	8·7	12·0	11·2	22·2	81	·	·	2	1·6	1·8 B
Knipe	25·5	6·7	10·0	66	7·5	12·7	7·8	17·1	74	·	·	1	1·2	3·3 A
Podnet	22·3	6·3	6·7	64	4·7	11·9	10·8	25·6	70	6·2	15·5	2	2·3	2·0 B
Cacer	5·7	6·0	7·3	60	9·5	17·3	8·5	23·5	70	·	·	1	1·6	1·3 B
Black Beck Moss	3·5	6·0	7·0	70	9·3,	15·7	11·3	31·0	79	10·4	23·2	3	1·9	1·0 B
Green Hows Reservoir	12·4	5·7	4·9	67	8·4	12·2	6·9	12·7	71	·	·	1	1·5	−0·8 C
New	*c.* 10·0	5·7	8·2	56	5·3	10·5	8·2	20·3	61	·	·	1	1·5	2·9 B
Batemanfold 1	0·9	5·6	8·0	58	12·1	21·5	15·4	42·2	103	·	·	3	2·7	2·4 B
Blelham Fishpond	3·4	5·5	8·1	·	10·1	18·9	10·9	27·5	84	15·5	40·7	3	2·0	2·6 B
Gill Head Reservoir	36·8	5·2	5·6	62	5·3	7·3	5·7	9·5	59	6·0	10·5	1	1·1	0·4 B
WMFP 3	0·9	5·2	6·1	65	5·3	7·1	8·6	19·3	77	·	·	2	1·7	0·9 B
Wharton	15·3	5·1	7·2	54	7·1	16·1	8·7	20·5	73	9·1	19·8	1	1·7	2·1 B
School Knotts	4·9	5·0	8·3	57	7·2	13·2	7·5	17·7	63	·	·	1	1·5	3·3 A
WMFP 1	3·8	·	·	·	4·8	5·3	6·4	9·5	66	·	·	2	·	·
Brigstone 2	3·0	4·4	8·1	45	12·2	27·0	·	·	·	·	·	1	·	3·7 B
Lost	1·9	4·3	4·9	52	5·5	12·0	·	·	·	·	·	3	·	0·6 B
Nor Moss	18·1	4·3	3·8	56	6·4	10·7	10·5	30·0	82	·	·	3	2·4	−0·5 C
Gill Head Fishpond	5·0	4·2	3·6	59	4·4	4·8	4·7	9·4	52	4·9	9·3	2	1·1	−0·6 C
Lindeth	9·6	4·0	7·9	56	5·5	12·1	4·2	12·0	51	·	·	3	1·4	3·9 A
Arnside	*c.* 10·0	4·0	6·8	50	5·0	8·54	5·7	18·2	61	·	·	1	1·4	2·8 A
WMFP 2	0·9	·	·	·	4·0	7·3	7·6	15·8	74	·	·	2	·	·
Wray Mires	13·9	3·8	4·3	49	5·3	8·0	5·6	13·2	58	5·6	11·4	1	1·5	0·5 B
Hodson	5·7	3·8	4·8	52	4·0	6·5	5·7	12·0	57	·	·	1	1·5	1·0 B
Robinson	3·9	3·8	4·1	51	4·6	8·6	6·5	17·7	62	7·0	17·5	2	1·7	0·3 B
Tarn Hows	171·1	3·6	6·0	49	6·2	9·3	7·0	14·5	70	4·3	9·2	1	1·9	2·4 B
Moss Eccles	42·1	3·4	3·6	48	5·1	8·6	6·0	14·8	61	4·8	7·2	2	1·8	0·2 B
Wise Een	52·7	3·3	3·4	48	3·7	6·6	5·1	8·7	52	4·8	8·6	1	1·5	0·1 B
Three Dubs	19·2	3·0	2·1	·	3·0	3·9	4·9	8·8	59	5·2	7·5	1	1·6	−0·9 C
Brigstone 1	7·5	2·7	3·8	40	5·7	10·5	·	·	·	·	·	1	·	1·1 B
Goosefoot	4·7	2·4	2·0	42	4·1	6·5	3·3	4·3	49	·	·	1	1·7	−0·4 C
Lingmoor	6·2	1·9	0·7	42	3·2	4·6	2·2	2·0	34	·	·	2	1·7	−1·2 C
Blea	44·5	1·8	0·9	35	2·6	4·7	2·2	2·4	34	·	·	1	1·4	−0·9 C
Harrop	18·0	1·8	0·5	36	2·4	2·5	·	·	·	·	·	1	·	−1·3 C
Pools:														
Brathay Quarries 2	0·01	12·2	15·3	102	12·9	20·0	10·8	31·0	86	·	·	·	1·2	4·5 A
Brathay Quarries 5	0·9	10·7	27·6	85	9·6	33·5	18·5	50·9	142	·	·	·	1·9	18·0 A
Outgate Quarry	0·03	6·6	5·2	90	12·9	15·4	·	·	·	·	·	·	·	−1·4 C
School Knotts Moss	0·01	6·1	14·2	61	9·7	23·8	·	·	·	·	·	·	·	8·1 A
Torver Moss	0·8	·	·	·	6·0	10·8	8·0	21·3	67	5·6	10·5	·	·	·
Barngates Quarry	0·2	5·0	8·1	48	6·6	12·3	6·7	15·7	52	·	·	·	1·3	3·1 A
Wise Een Pool	0·01	4·0	6·4	48	9·7	24·4	·	·	·	·	·	·	·	2·4 B
Sweetenthwaite	1·1	3·8	1·2	58	5·3	4·9	5·1	6·1	60	·	·	·	1·4	−2·6 C
Undermillbeck 2	0·8	·	·	·	4·2	5·4	3·1	1·5	45	·	·	·	·	·
Birket Houses	0·2	·	·	·	4·4	6·6	2·8	3·7	44	·	·	·	·	·
Ustick Moss	11·2	2·6	1·8	49	4·6	5·7	5·2	10·1	56	4·0	10·5	·	2·0	−0·8 C
Iron Keld	0·06	·	·	·	2·5	5·8	4·5	10·0	53	·	·	·	·	·
Stephen How	0·9	·	·	·	2·0	2·3	1·6	0·3	36	·	·	·	·	·
Loughrigg 10	2·9	1·2	1·0	34	3·0	5·3	·	·	·	·	·	·	·	·
Green Pool	0·9	0·8	Nil	61	1·7	1·5	1·7	Nil	53	·	·	·	2·1	−0·8 C

Table 6. *The relation between lowest/highest calcium ratio and botanical stage. The figures show the number of tarns*

	Ratio		
	1·1–1·5	1·6–1·9	2·0–3·0
Botanical stage 1	12	6	0
2	1	7	2
3	1	1	5

There are 21 tarns with 5·0 mg. calcium/l. or more in the wet winter sample, and 20 with less. Thirteen out of the 15 tarns lying to the east of Windermere (Fig. 1) are in the higher group, but there is no explanation of this higher general level of calcium concentration. Elsewhere a high calcium concentration is due to narrowly local causes.

The high value of Rather Heath 6 may be in part attributable to lime on the surrounding fields. Cleabarrow Tarn and the Clay Pond are also surrounded by grassland of sufficiently good quality to warrant occasional dressings of lime, but the rest are surrounded by moorland and rough sheep pasture which is not worth treating.

(*c*) *History and method of collecting*

A number of tarns and pools from which collections had been made during an earlier investigation were selected for standard collections, about half of which had been made in 1939 and 1940 when war interrupted the work. In 1946 all the selected tarns and pools were revisited and a standard collection made in each.

It is important to say more about this selection or a misleading impression may be created. Every body of water where snails were found by casual collection was selected for standard collecting. This included almost all the artificial tarns and a few probably atypical pools, and excluded most of the natural tarns and nearly all the pools. A few of these negative places were selected as examples (Table 7), but that there were many more must be borne in mind before a true picture of the distribution of fresh-water snails in the Lake District is possible. Harrop, Lingmoor and Blea Tarns were selected as typical natural tarns. Casual collections have been made in fifteen at one time or another, but no gastropods recorded except in Red Tarn, Helvellyn, where *Limnaea peregra* was taken in a trawl dragged across the tarn.

Green Pool, Sweetenthwaite, Undermillbeck 2, and Stephen How may be taken as typical of the large number of pools lying at all altitudes in the Lake District.

All the collections were made with a pond-net, for gastropods were usually so sparse that the use of a grab or any other quantitative instrument was impracticable. The standard was a collection made in 60 min. It is not claimed that this is an accurate quantitative method, and the objections to it as such scarcely need pointing out. The filtering powers of the net vary greatly according to whether or not there is much filamentous green alga, the amount of debris which accumulates in the net affects the time which has to be spent sorting, and above all there is the uneven distribution of the snails themselves, which invariably are scarce in some regions and concentrated in others. To obviate this a complete tour of the tarn or pool was made during the course of the hour spent collecting. If a tarn was very big, an hour might be spent on each of two sides and, if a pool was very small, less than an hour was sometimes devoted to it. The catch from such localities has been divided or multiplied by the appropriate factor to bring it to the equivalent of 1 hr. work before being set out in Table 7. The figures obtained by this standard method of collecting have a certain comparative value and are preferable to adjectives. Boycott, for example, records taking 620 specimens 'in one sweep of a small scoop'; presumably he would have called this very abundant. It is about the total of my biggest catch in one hour, and relative to other catches this might also be referred to as very abundant.

All the standard collections were made in July, August, September, or early October.

Fig. 1 shows the tarns and pools studied; and the drainage areas, which appear of no importance. In order to avoid too much detail on one map the 500 and 1000 ft. contours, between which most of the tarns and pools lie, are shown on Fig. 5.

(*d*) *Results*

All the collecting results are set out in Table 7; figures are given for the standard collections, but presence only is recorded for the earlier casual collections. The tarns are arranged in descending order of calcium concentration, the analyses being those of February 1948. Column 3 repeats the last column of Table 5.

Before the records are analysed, there are three preliminaries: first, to examine what changes in composition the populations have undergone during the 10 years of observation; secondly, to comment on numerical differences between the two sets of standard collections; and thirdly, to describe the history of one tarn in which changes at present inexplicable have taken place.

Table 8 shows the gains and losses when the different collections are compared. Gains are obviously of little significance when a standard and a casual collection are compared and they have been omitted; in one locality, however, special circumstances justify the assertion that a gain has taken

Table 7. *Records from tarns and pools*

Figures for snails caught have been converted into a standard 'number caught in 1 hr.'

Locality	Actual Ca	Alk. minus Ca class	Area (1000 sq.yd.)	Botanical stage	Year (19---)	*Limnaea pereger*	*Planorbis albus*	*P. contortus*	*Physa fontinalis*	*Valvata piscinalis*	*Limnaea palustris*	*L. glabra* (Müll.)	*L. stagnalis* (L.)	*Planorbis complanatus*	*P. crista* (L.)	*P. spirorbis*	*Limnaea truncatula* (Müll.)
Tarns:																	
Rather Heath 6	16·6	A	7·7	2	36	+	+	.	.	.	+	.	.	+	.	.	+
					40	10	50	.	.	.	4	.	.	1	.	.	.
					46	4	241	.	.	.	69	.	.	5	.	.	10
Rather Heath 1	15·2	A	25·2	1	40	.	33	.	.	.	9	.	2	.	18	.	.
					46	3	65	.	.	.	16	.	4	17	6	.	.
Rose Castle	9·6	A	5·8	2	38	.	+	.	.	.	.	.	.	.	.	.	.
					39	.	17	.	.	.	.	.	.	.	.	.	.
					46	.	26	.	.	.	.	.	.	.	.	.	.
Crook Upper	9·4	A	2·3	2	36	+	.	.	.	.	.	.	.	.	.	.	.
					40	28	49	.	.	.	.	.	.	.	1	.	.
					46	43	24	.	.	.	.	.	.	.	.	.	.
Cleabarrow	9·2	A	6·6	1	38	.	+	.	.	.	+	.	.	+	.	.	.
					46	58	29	.	.	.	1	.	.	.	.	.	.
Little Ludderburn	8·6	B	40·0	3	39	.	+	.	.	.	.	.	.	.	.	.	.
					46	34	43	.	.	.	1	.	.	.	.	.	.
Crook Lower	8·0	B	9·0	3	36	+	.	.	.	.	.	.	.	.	.	.	.
					40	4	44	.	.	.	.	.	.	.	.	.	.
					46	79	15	.	.	.	9	.	.	.	.	.	.
Clay Pond	7·6	B	0·7	1	35	+	.	.	.	.	.	.	.	.	.	.	.
					46	15	374	.	.	.	.	.	.	.	.	.	.
Slew	7·1	B	6·2	2	36	+	.	.	.	.	.	.	.	.	.	.	.
					46	4	41	.	.	.	.	.	.	.	.	.	.
Knipe	6·7	A	25·5	1	37	+	.	.	.	.	.	.	.	.	.	.	.
					38	6	3	.	.	.	.	.	.	.	.	.	.
					46	24	26	.	.	.	.	.	.	.	.	.	2
Podnet	6·3	B	22·3	2	36	.	+	.	.	.	.	.	.	.	.	.	.
					39	1	3	.	.	.	.	.	.	.	.	.	.
					46	4	26	.	.	.	1	.	.	7	.	.	.
Cacer	6·0	B	5·7	1	36	.	+	.	.	.	.	.	.	.	.	.	.
					46	.	81	.	.	.	6	.	.	.	.	.	.
Black Beck Moss	6·0	B	3·5	3	36	+	.	.	.	.	.	.	.	.	.	.	.
					40	80	.	.	.	.	.	.	.	.	.	.	.
					46	152	.	.	.	.	.	2	.	.	.	.	.
Green Hows Reservoir	5·7	C	12·4	1	36	+	.	.	.	.	.	.	.	.	.	.	.
					46	148	.	.	.	.	.	.	.	.	.	.	.
New	5·7	B	*c.* 10·0	1	35	+	+	.	.	.	.	.	.	.	.	.	.
					38	6	80	.	.	.	.	.	.	.	.	.	7
					46	166	338	.	.	.	2	.	.	.	6	.	.
Batemanfold 1	5·6	B	0·9	3	40	73	.	.	.	.	.	.	.	.	.	.	.
					46	182	.	.	.	.	11	.	.	.	.	.	.
Blelham Fishpond	5·5	B	3·4	3	38	!	+	.	.	.	.	.	.	.	.	.	+
					46	23	56	.	.	.	.	.	.	.	.	.	.
Gill Head Reservoir	5·2	B	36·8	1	38	1	5	.	.	.	.	.	.	.	.	.	.
					46	213	251	.	.	.	.	.	.	.	.	.	1
Wray Mires Fishpond 3	5·2	B	0·9	2	39	2	.	.	.	.	.	.	.	.	.	.	.
					41	*c.* 200	.	.	.	.	.	.	.	.	.	.	.
Wharton	5·1	B	15·3	1	36	!	.	.	.	.	+	.	.	.	.	.	.
					39	.	16	.	1	3	1	.	.	.	.	.	.
					46	13	35	.	71	2	175	.	.	.	.	.	.
School Knotts	5·0	A	4·9	1	36	.	.	.	.	+	?	.	?	.	.	.	.
					37	.	!	!	.	.	.	!	!	.	.	.	.
					38	.	.	.	.	.	.	.	+	.	.	.	.
					40	.	.	.	.	.	.	.	33	.	.	.	.
					46	.	.	.	.	.	.	4	.	.	.	.	.

Wray Mires Fishpond 1	.	.	3·8	2	36	.	.	.	.	.	.	.	.	.	.	.	.	.
					39	5	.	.	.	.	.	.	.	.	.	.	.	.
Brigstone 2	4·4	B	3·0	1	36	+	.	.	.	.	.	.	.	.	.	.	.	.
					46	31	.	.	.	.	.	.	.	.	.	.	.	.
Lost	4·3	B	1·9	3	39	.	25	.	.	.	.	.	.	.	.	.	.	.
					46	.	5	.	.	.	.	.	.	.	.	.	.	.
Nor Moss	4·3	C	18·1	3	36	+	.	.	.	.	.	.	.	.	.	.	.	.
					40	22	.	.	.	.	.	2	.	.	.	.	.	.
					46	216	.	.	.	.	.	.	.	.	.	.	.	.
Gill Head Fishpond	4·2	C	5·0	2	36	+	.	.	.	.	.	+	.	.	.	.	.	.
					39	34	.	.	.	.	.	.	.	.	.	.	.	.
					46	459	.	.	.	.	1	.	.	.	.	.	.	.
Lindeth	4·0	A	9·6	3	37	+	+	.	.	.	.	.	.	.	.	.	.	.
					46	2	12	.	.	.	1	.	.	1	.	.	.	.
Arnside	4·0	A	*c.* 10·0	1	38	+	+	.	.	.	.	.	.	.	.	.	.	.
					40	132	105	.	.	.	.	.	.	.	.	.	.	.
					46	353	537	.	.	.	.	.	.	.	.	.	.	.
Wray Mires Fishpond 2	.	.	0·9	2	37	+	.	.	.	.	.	.	.	.	.	.	.	.
					39	24	.	.	.	.	.	.	.	.	.	.	.	.
Wray Mires	3·8	B	13·9	1	36	.	+	.	.	.	.	.	.	.	.	.	.	.
					46	54	218	2	.	1	4	.	.	.	.	.	.	.
Hodson	3·8	B	5·7	1	40	59	.	.	.	.	.		.	.	.	.	.	.
					46	58	.	.	.	.	.	.	.	.	.	.	.	.
Robinson	3·8	B	3·9	2	36	+	.	.	.	.	.	.	.	.	.	.	.	.
					40	24	.	.	.	.	.	.	.	.	.	.	.	.
					46	228	.	.	.	.	.	.	.	.	.	.	.	.
Tarn Hows, east side	3·6	B	171·1	1	39	9	21	13	7	6	.	.	.	.	1	.	.	
west side					46	.	57	47	6	2	.	.	.	.	.	.	.	1
					46	1	150	.	1	.	6	.	.	.	.	.	.	.
Moss Eccles	3·4	B	42·1	2	36	+	.	.	.	.	.	.	.	.	.	.	.	.
					46	56	.	.	.	.	.	.	.	.	.	.	.	.
Wise Een,	3·3	B	52·7	1	38	.	+	+	.	.	+	.	.	.	.	.	.	.
west side					46	6	10	.	.	.	56	.	.	.	.	.	.	.
east side					46	.	46	1	.	.	12	.	.	.	.	.	.	.
Three Dubs	3·0	C	19·2	1	36	+	.	.	.	.	.	+	.	.	.	.	.	.
					46	2	.	.	.	.	.	.	.	.	.	.	.	.
Brigstone 1	2·7	B	7·5	1	36	.	.	.	.	.	.	.	.	.	.	.	.	.
					39	.	.	.	.	.	.	.	.	.	.	.	.	.
					46	.	.	.	.	.	.	.	.	.	.	.	.	.
Goosefoot	2·4	C	4·7	1	36	.	.	.	.	.	.	.	.	.	.	.	.	.
					46	.	.	.	.	.	.	.	.	.	.	.	.	.
Lingmoor	1·9	C	6·2	2	36	.	.	.	.	.	.	.	.	.	.	.	.	.
					40	.	.	.	.	.	.	.	.	.	.	.	.	.
					46	.	.	.	.	.	.	.	.	.	.	.	.	.
Blea (Wrynose)	1·8	C	44·5	1	36	.	.	.	.	.	.	.	.	.	.	.	.	.
					46	.	.	.	.	.	.	.	.	.	.	.	.	.
Harrop	1·8	C	18·0	1	36	.	.	.	.	.	.	.	.	.	.	.	.	.
					46	.	.	.	.	.	.	.	.	.	.	.	.	.
Pools:																		
Brathay Quarries 2	12·2	A	0·01	.	46	.	7	.	.	.	.	.	.	.	.	.	.	.
Brathay Quarries 5	10·7	A	0·9	.	46	.	300	.	.	.	.	.	.	.	.	.	.	.
School Knotts Moss	6·1	A	0·01	.	38	.	.	.	.	.	.	+	.	.	.	.	.	.
Wise Een Pool	4·0	B	0·01	.	38	.	.	.	.	.	.	.	.	.	.	.	+	.
					40	.	.	.	.	.	.	.	.	.	.	.	+	.
11 pools					←						Nil							→

place. The Clay Pond, being close to Wray Castle, is visited frequently by collectors for the supply department and by classes, and the fact that *Planorbis albus* was not recorded till the standard collection of 1946 indicates that it was a recent arrival then; quite incidentally the laboratory steward, Mr G. J. Thompson commented on its appearance.

Six of the ten species in Table 8 were taken in 1946 in places where they had not been taken before the war. There was one such gain by *Limnaea pereger* but the place was Wharton Tarn, where the species had been taken earlier in the casual collections; its 'absence' in 1939 was evidently due to scarcity, and its 'reappearance' in 1946, when it was still scarce, does not represent a true gain. The finding in 1946 of *L. palustris* in six tarns where it had not been before suggests an extension of range during the war years. The rest of the gains are among the species found in small numbers in few tarns.

figures for *Planorbis albus* are 10 out of 13. In several tarns the increase in the number caught in 1 hr. was great (Table 7). Collections made in Nor Moss illustrate this rise (Table 9); number per hour is shown though collecting usually lasted for 30 min. only. The catch was returned to the water after counting. No explanation of the increase is offered.

In two tarns, New and Podnet, *P. albus* was so numerous in 1935 and 1936 that the recorded comments on its abundance leave no doubt that it had decreased greatly when the standard catch was made. It may be significant that both tarns had been in existence only 3 or 4 years at the time of the first collection.

School Knotts Tarn was omitted from the foregoing discussion and is omitted from the analysis which follows, because collecting in it yielded results so unlike those in any other tarn. In 1933 or 1934, Mr K. Shepherd recalls having seen commonly a

Table 8. *Changes in the snail population of tarns as indicated by a comparison of casual collections* 1935–8 *with standard collections* 1939–40, *and standard collections* 1939–40 *with standard collections* 1946

		Limnaea pereger	*Planorbis albus*	*P. contortus*	*Physa fontinalis*	*Valvata piscinalis*	*Limnaea palustris*	*L. glabra*	*Planorbis complanatus*	*P. crista*	*Limnaea truncatula*
Gains	Standard to standard	1	0	0	0	0	6	1	2	1	4
Losses	Casual to standard	1	0	0	0	0	1	1	1	0	2
	Standard to standard	0	0	0	0	0	0	1	0	2	0
No. of tarns from which the species was recorded		32	22	3	2	3	15	3	5	4	6

Table 9. *Numbers of* Limnaea pereger *collected in 1 hr. in Nor Moss*

Date	11 July 1939	31 Oct. 1939	9 Apr. 1940	21 May 1940	9 July 1940	21 Aug. 1940	23 Aug. 1947
Number	42	56	26	14	22	28	216

Losses are few. The disappearance of *L. pereger* from Wharton Tarn has already been discussed. *L. palustris* was not found in one tarn where it had been previously. Most of the losses, like most of the gains, are among the rare and scarce species, and it is probable that their low numbers rendered it a matter of chance whether they were collected during any one visit, as did the low numbers of *L. pereger* in Wharton Tarn. Possibly some of them, being species with good powers of dispersal near the edge of their range, are constantly invading fresh tarns but dying out because conditions are unfavourable.

The general picture is one of stability, and the changes in the composition of the population of the various tarns are less than those in the ponds at Aldenham studied by Boycott (1930).

L. pereger was more abundant in 1946 than in 1939 and 1940 in 16 out of 18 tarns, and the corresponding

large snail, which could only have been *Limnaea stagnalis*. In 1936 it was very scarce, but by 1938 it was abundant once more. Then it waned again and an hour's collecting in 1946 did not secure it. Small numbers of *Valvata piscinalis*, *Planorbis albus* and *P. contortus* have been taken on one occasion each. *Limnaea glabra*, though not abundant, has turned up fairly constantly. At present there is no explanation of these facts though there is one observation which is suggestive. In about 1939, Mr Shepherd first noticed in the tarn a trout which he estimated to be 1½–2 lb. in weight. It continued to flourish till 1944, when it was found dead, its weight then being some 3½ lb. The tarn is not large, there is no thick vegetation, and one big fish—a two-pounder is big for a Westmorland tarn—might perhaps reduce a snail population to a low level or even extinction. School Knotts is not preserved as a fishing tarn and this

solitary fish may have been introduced by someone hoping for sport later, as this is quite a common local practice.

Also worth recording is that School Knotts Tarn is within strolling distance of the big holiday and residential area of Windermere and Bowness, and it would be the obvious choice of anyone seeking a natural piece of water for transplantation experiments or a home for the inmates of an aquarium which could no longer be kept.

In the remaining tarns there have been no such bewildering changes of population. The most satisfactory method of analysis has been found to be to take each species and look for common features among the tarns and pools in which it does and does not occur.

Limnaea pereger has been found in none of the pools, but in more tarns than any other species, being absent from eight only out of a total of forty. Five of these eight are the five in which the lowest concentration of calcium is below 3 mg./l. (Fig. 4). The remaining three are all woodland tarns completely surrounded by trees. In the fourth tarn of this type, Slew, *L. pereger* is very scarce.

But 3 mg./l. is probably a threshold concentration only in the conditions obtaining in Lake District tarns. The value in Ennerdale on 18 November 1947 (Table 2) was 2·3, and this may be another example of large size compensating for low calcium. Boycott quotes a record of *L. pereger* in less than 1 mg. calcium/l., but does not mention the locality. On 30 March 1948 the author took *L. pereger burnetti* in Loch Skene, Dumfriesshire, and brought back an outflow sample in which Mr Mackereth found 1·8 mg. calcium/l.

Planorbis albus occurs in 22 tarns and also in two pools, both deep quarry pools in a wood. Neither of the latter has any rooted vegetation, and the bottom of each is covered to a depth of several feet with dead leaves. These woodland conditions are evidently not unfavourable for *P. albus*, as they are for *Limnaea pereger*, and it is found in all four woodland tarns, though not in great numbers in any of them.

The development of vegetation appears to affect *Planorbis albus* adversely, as is shown in Table 10. *P. albus* is absent from three out of eight tarns at botanical stage 3, and there are reasons for believing that these three have been in this stage longer than the others.

It is likely that calcium is a factor in the ecology of *P. albus*, though there is no clear limiting value as for *Limnaea pereger*. A lowest value of 5 mg. calcium/l. is a convenient starting-point for analysis because there are 19 tarns with more and 21 with less. Fig. 4 shows that *Planorbis albus* is absent from four of the 19 tarns in the higher category; two of these are stage 3 tarns. A third, Great Green Hows, is the only one of the 19 in class C, and *P. albus* is absent from every tarn with this particular relationship of calcium and alkalinity. It is, moreover, present in every tarn belonging to class A, so this at present inexplicable factor is evidently important in its ecology. Wray Mires Fishpond 3, the fourth tarn lacking *P. albus*, is one of the smallest tarns in the group, and this may be significant, though, as will be shown later, it has not been possible to assess how important a factor size is.

Table 10. *Numbers of* Planorbis albus *in relation to the botanical stage of the tarn*

Botanical stage	Total tarns	Total *albus*	No. of tarns with *albus*	No. of *albus* per tarn	No. of tarns in which more than 100 *albus* collected in 1 hr.
			(1) All tarns		
1	20	2150	12=60%	107	6
2	12	358	5=42%	30	1
3	8	131	5=62%	16	0
			(2) Omitting tarns with less than 3 mg. calcium/l. and those in class C		
1	14	2150	12=85%	154	.
2	9	358	5=55%	40	.
3	7	131	5=71%	19	.

Of the 21 tarns with a minimal calcium concentration of less than 5 mg./l., seven harbour *P. albus*. Two are the only ones in the group belonging to class A. Two, Wise Een and Tarn Hows, are the largest by a fair margin, and Wray Mires, being near and connected with Wise Een, must be included with it. Lost Tarn is a woodland tarn, and abundance of dead leaves appears to favour *P. albus*. Finally Podnet Tarn is in this group only on the strength of the figure for January 1947; had it been classed on the 1948 figure, which was the lowest for most tarns, it would be in the other group. Some small local effect may have produced the low result in 1947.

Size has already been mentioned several times and

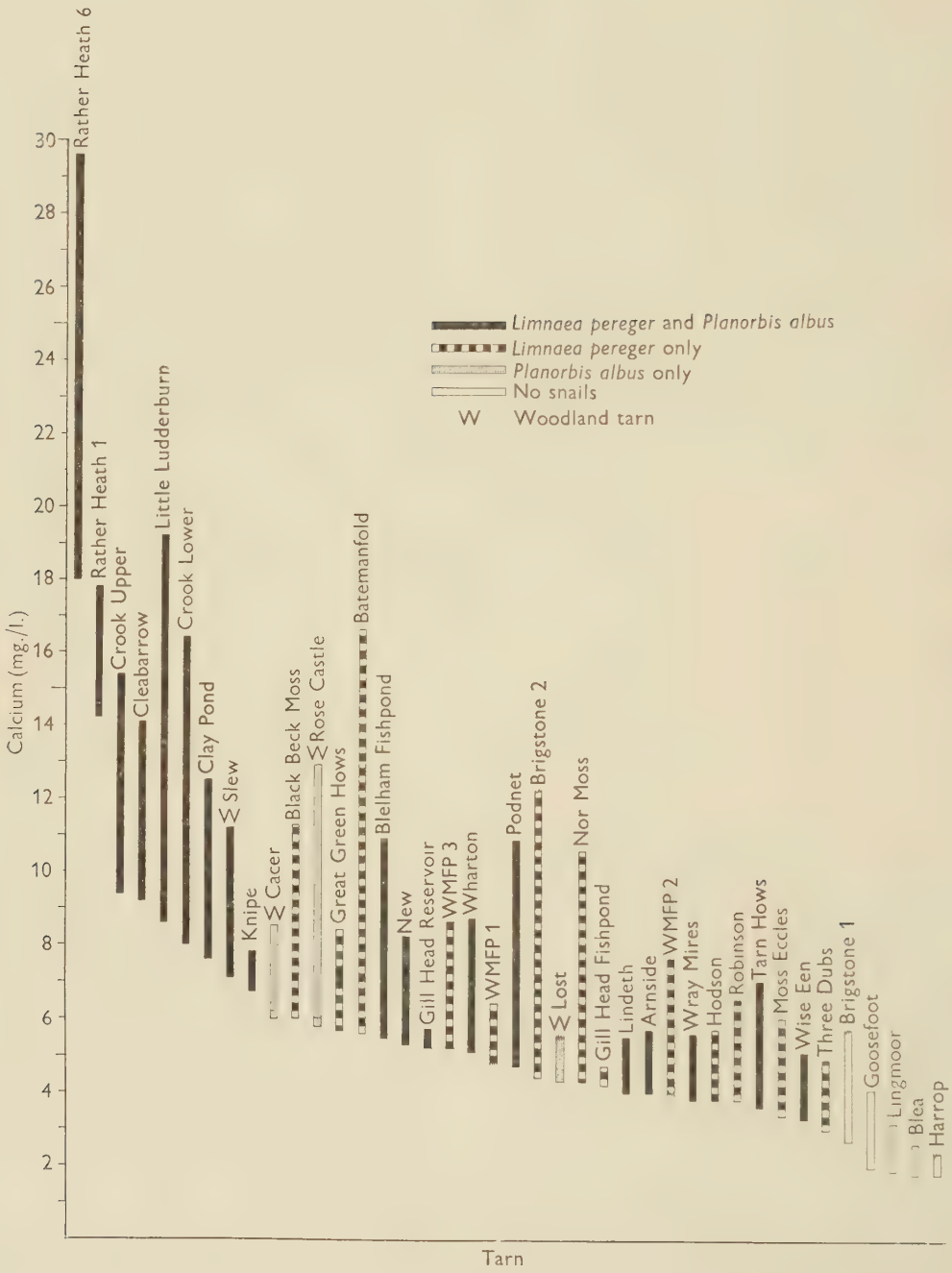


Fig. 4. The highest and lowest calcium concentrations, and the occurrence of *Limnaea pereger* and *Planorbis albus* in tarns.

must be examined. If we discard nine tarns with more than 6 mg./l. of calcium, all of which harbour *P. albus*, and five with less than 3 mg./l. none of which harbours any snails, the remainder are those near the threshold, where a small variation of any factor may be decisive. Ten tarns are less than 5000 sq.yd. in area and two of them harbour *P. albus*; 16 are bigger than this and 11 harbour *P. albus*. These figures are just significant according to the χ^2 test, but when factors already discussed are taken into account, it is found that few of the tarns are strictly comparable and there are not enough data on which to base any conclusions about size.

Valvata piscinalis, Physa fontinalis and **Planorbis contortus** constitute a group which occurs in four tarns; the numbers caught in standard collections (added together if there was more than one) are shown in Table 11. The species list is not identical for any of these tarns, but the fauna has none the less a distinctive facies and gives good grounds for treating the three species as a group. *Limnaea pereger* is present in moderate numbers in Wray Mires Tarn, but in the other three it is scarce and in each it has on one occasion not been taken at all in a standard collection (Table 7). Paucity of *L. pereger* is, therefore, one characteristic of this association of species. Another is presence of *L. palustris*. This snail is found only in six tarns out of the 26 to the west of Windermere; four of these constitute the group under discussion. Moreover, the number of specimens caught in them includes the highest and the two but highest totals recorded in any tarn.

Table 11. *Details of catches in four tarns*

	Limnaea pereger	*Planorbis albus*	*P. contortus*	*Physa fontinalis*	*Valvata piscinalis*	*Limnaea palustris*	*Planorbis crista*	*Limnaea truncatula*
Wray Mires	54	218	2	.	1	4	.	.
Wise Een	6	56	1	.	.	68	.	.
Wharton	13	51	.	72	5	176	.	.
Tarn Hows	10	228	60	14	8	6	1	1

Wise Een Tarn flows into Wray Mires, the two are only 170 yd. apart, and they must therefore be treated as one. Tarn Hows receives drainage from the Coniston limestone and Wharton Tarn lies near this formation; but Wise Een does not, and therefore this is not a common factor. Tarn Hows has the greatest and Wise Een the next greatest surface area in the whole series, and the fact that the mollusc species are all found in lakes suggests that some feature connected with size is the explanation of their presence in the three tarns. But the third, Wharton, is not particularly large. It is, however, peculiar in one respect. It is a natural tarn and at some time an attempt has been made to drain it, or at least lower the level, by cutting a channel through the rock surrounding it. The effect of this was to lower the level by 6–8 ft., though, since most of the depression containing the tarn has steep sides, the reduction of surface area was not great. The walls of the cut have since collapsed, filling it up with rubble, and the effect of this was to raise the level of the tarn by a foot or so, and also to cause a great increase in level after heavy rain, since the water, seeping through the blocked channel, cannot run off quickly. Presumably the flushing effect of rain is less than in other tarns, where there is little rise in level and the water escapes rapidly. It may be postulated that a large tarn is chemically more stable than a smaller one, as its waters will be diluted less by heavy rain; and that the peculiar conditions of Wharton Tarn achieve a comparable result. But such analyses as have been made do not support this hypothesis.

Limnaea palustris occurs in 10 out of the 14 tarns which lie to the east of Windermere but in six only out of 26 on the other side. There are several faunistic peculiarities in the tarns to the east of Windermere, and the concentration of calcium is unaccountably high. Of the six tarns on the west side, four have been discussed in the preceding section; they harbour three species otherwise confined to lakes. The remaining two, Lost and Cacer, both have a greater volume of water flowing through them than most and probably associated with the silting which this entails is the presence in fair numbers of a water-bug, *Corixa fossarum* Leach, which is common in the most advanced lakes but generally rare in tarns.

This analysis leads only to a vague conclusion that *Limnaea palustris* is found in tarns where conditions are good, and this is borne out by its occurrence in tarns where the number of other snail species is high (Table 12).

Limnaea glabra is the one gastropod which, according to Boycott, may be calcifuge. It is typically found in small, often temporary pools, 'where the ground is harsh and poor'. In the present survey it has been taken only in five places, including School Knotts Tarn. Near this tarn is a small pool, School Knotts Moss, which is thickly overgrown with *Sphagnum*, but which had an unexpectedly high calcium concentration, 6·1 mg./l., in January 1948.

It is the only place where *L. glabra* has been taken abundantly. Of the remaining three places, two are stage 3 botanically and the third, though only stage 2, has a bog at the inflow and a fairly extensive development of *Sphagnum* round the edges. The inexplicable thing about this species is why, if these poor conditions really provide a favourable habitat, it is not much more widespread.

Table 12. *The association between* Limnaea palustris *and the total number of snail species in tarns*

No. of species	1	2	3	4	5	6	7	8
No. of tarns	10	8	7	4	4	1	0	1
No. of tarns with *L. palustris*	0	3	3	4	4	1	0	1

Limnaea stagnalis in School Knotts Tarn has been discussed above (p. 138). If Rather Heath 6 be excluded on the grounds that its high value may be a temporary effect due to lime on the surrounding land, Rather Heath 1 has a calcium concentration which is the highest and the only one to approach the critical value of 20 mg./l. That it should be the only tarn from which the calciphile snail, *L. stagnalis*, has been recorded regularly is, therefore, to be expected.

Planorbis complanatus is also a calciphile in Boycott's classification, and its occurrence in five tarns (Fig. 5) is, therefore, unexpected; though its numbers in all but Rather Heath 1 are small, and its appearances and disappearances frequent (Table 8), which may indicate that it has efficient dispersal and is constantly reaching new places only to die out in unfavourable conditions. It is confined to the east side of Windermere where the general trend of calcium concentration is higher than elsewhere, but it is not restricted to tarns with a high calcium concentration. It occurs, for example, in Lindeth Tarn which, with 4·0 mg./l., comes quite low in the series.

Planorbis crista has been found in Tarn Hows, of which some of the inflowing streams have a high calcium concentration (Table 4, p. 132), and in three tarns to the east of Windermere, all with a high calcium concentration (Fig. 5).

Planorbis spirorbis has been found in two lakes in the north part of the Lake District (Table 2) and in one pool in the south part, where it has been known since 1938. This locality, Wise Een Pool, is a slight hollow in which there has been as yet no development of peat, which is probably why, unlike most pools, it dries up in summer. When it is full, the calcium concentration is rather high.

Boycott describes how *P. spirorbis* occurs in poor temporary places and also in large bodies of water, and suggests that competition may exclude it from places intermediate in size.

Limnaea truncatula is not included among the aquatic species by Boycott.

Viviparus (Paludina) fasciatus (Müll.) was found when Scale Tarn, near Wise Een, was drained in December 1948. The tarn had been empty before the war and, when refilled, it had been stocked with snails in 1939. *Limnaea pereger* had been the species ordered but evidently some *Viviparus* were included in the consignment. It was surprising to find that the snails had not only survived, but done well, for the total number was fair, and some specimens were well grown. Unfortunately, Scale Tarn was dry when routine examinations began and consequently it was not included in the regular series.

4. The fresh-water limpets

The two limpets, as already stated, have not been studied as carefully as the other gastropods, since a different collecting technique is necessary to obtain them, and they are therefore relegated to a separate section.

Ancylastrum fluviatile (Müll.), being restricted to a hard substratum, is common in lakes and becks, but less common in tarns, in many of which there are no rock outcrops or stony stretches. In Three Dubs Tarn, for example, it is abundant on, but confined to, the dam, which is of concrete. It occurs in Outgate Quarry, a tiny pool with a rocky and stony bottom and hardly any higher vegetation. The pool is fouled a little by cattle which come to drink.

Ancylus lacustris is recorded only from Windermere, where it is abundant on *Phragmites* stems, and Brathay Quarries 5, a deep quarry pool with many dead leaves, but it is undoubtedly more widespread than this.

C. LAMELLIBRANCHS

Eleven species of *Pisidium* have been recorded. Every common species is associated rather often with every other common species, and it is not possible to do more than arrange them in two not very clearly defined groups, a 'lake' group and a 'tarn-pool' group (Table 13).

There is probably a genuine ecological distinction, though, had not most of the collections been made with a pond-net in shallow water, the habitat names might have been found inappropriate. Thus, as Table 14 shows, in Three Dubs Tarn, one of the few investigated both from the shore and with a boat, species of the 'lake group' were found at the deep-water stations.

Deep-water collections in Windermere are recorded by Humphries (1936), who found only two species at depths greater than 40 m. *P. cinereum* (*castertanum*) and *P. personatum*, both species which,

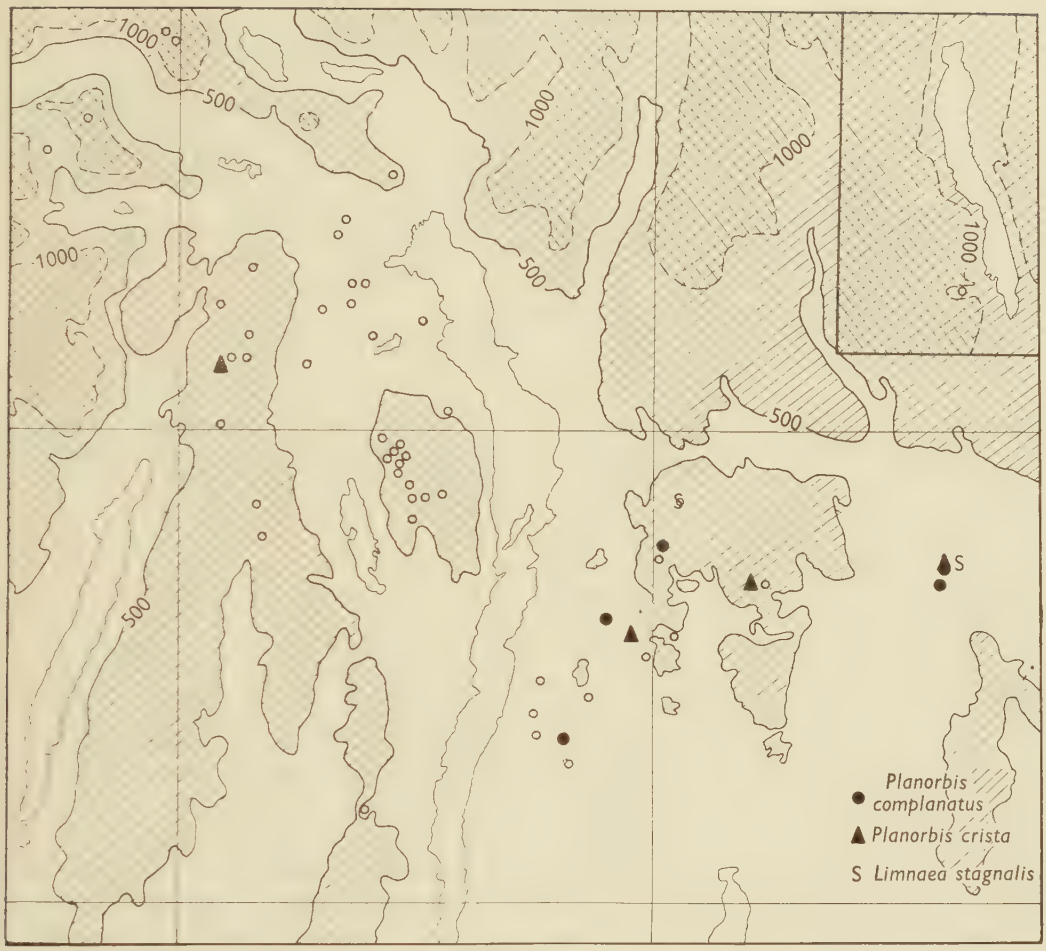


Fig. 5. The occurrence of *Planorbis complanatus*, *P. crista*, and *Limnaea stagnalis*. Contours in feet.

Table 13. *Total number of stations at which* Pisidium *has been recorded*

	Windermere	Tarns and pools	Total	No. of stations at which the only species
P. henslowanum (Sheppard)	0	1	1	0
P. conventus Clessin	0	2	2	0
P. cinereum Alder	3	21	24	10
P. personatum Malm	2	4	6	1
P. obtusale (Lamarck)	11	16	27	8
P. subtruncatum Malm	6	5	11	2
P. nitidum Jenyns	27	22	49	9
P. milium Held	10	4	4	0
P. hibernicum Westerlund	16	6	22	1
P. lilljeborgii Clessin	16	6	22	3
P. pulchellum Jenyns	3	0	3	0

on a basis of shallow-water collections, belong to the tarn-pool group.

P. henslowanum is listed as a calciphile by Boycott. A single specimen was taken in Blelham Fishpond, which has only a moderately high calcium content, though a bigger drainage area than most tarns.

P. conventus is known only from high mountain localities. In the present survey it was recorded from Red Tarn, near Helvellyn, 2356 ft. (716 m.) above sea-level, and from the nearby Brown Cove Tarn (Oldham, 1938).

A third species known to have restricted ecological requirements is *P. lilljeborgii* of which Boycott says: 'in clean gritty sand or silt, not mud'. It is not clear what distinction he makes between silt and mud. In Windermere *P. lilljeborgii* is the only species to occur more frequently on sandy bottoms with less than 10% organic matter than on bottoms with a higher

Table 14. *Collections of* Pisidium *in Three Dubs Tarn*

Date	Nature of station	Vegetation, etc.	*P. cinereum*	*P. personatum*	*P. obtusale*	*P. subtruncatum*	*P. nitidum*	*P. milium*	*P. hibernicum*	*P. lilljeborgii*
24 Mar. 1937	Deep water in middle	Peaty bottom, without vegetation	4	.	.	.	1	1	4	.
24 Mar. 1937	Deep water in middle	Peaty bottom, without vegetation	1	.	.	.	1	.	.	1
7 Aug. 1937	Deep water in middle	Peaty bottom, without vegetation	.	.	.	.	6	.	1	.
31 July 1936	Shallow water near margin	*Carex* bed	.	.	2	.	.	.	.	.
27 July 1936	Shallow water near margin	*Carex* bed	4	.	.	.	.	.	.	.
31 July 1936	Marginal marsh	*Sphagnum* and *Juncus*	14	.	14	.	.	.	.	.
7 Aug. 1937	Marginal marsh	*Sphagnum* and *Juncus*	2	.	2	.	.	.	.	.

value than this, but it is also recorded from localities with as much as 45% organic matter in the soil.

Of the rest Boycott writes: 'We may also construct a sort of hierarchy of gentility, starting with *personatum*, which lives in the slums through *obtusale*, *cinereum*, *milium*, *nitidum*, *subtruncatum*, *hibernicum* to *henslowanum*....' In the Lake District, the most difficult places to live in, 'the slums' to use Boycott's analogy, are probably high pools, and conditions become better in, successively, high tarns, low pools, and low tarns. Therefore *P. cinereum* should perhaps be put first, for it occurred in both places which yielded *P. conventus* and in several other high tarns such as Stickle, Harrop and Lingmoor (cf. Table 6), as well as in several high pools. In these places it was usually the only species. Humphries (1936) found it only between 30 and 60 m. in Windermere, though the present author has found it occasionally in shallow water. *P. personatum* is the other deep-water species in Windermere and was also found in Red Tarn, Helvellyn, but its other localities are two low tarns and one low pool. *P. obtusale* occurs in eleven low tarns and one low pool.

The data about the rest do not justify any comment on Boycott's order. Each species has been found abundantly in at least one tarn, but *P. nitidum* is the only one recorded from a pool.

Both *Sphaerium lacustre* (Müll.) and *S. corneum* are fairly widely distributed, but neither has been collected systematically. *S. lacustre* is sometimes abundant where there are many dead leaves.

Unio pictorum (L.) is recorded from the River Brathay near Ambleside by Standen (1909), and the same author records *Margaritifera margaritifera* (L.) near Ambleside; in the River Leven a little below Windermere; in the Greta at Keswick; in Chapel Beck which flows into Bassenthwaite; and also in the Rivers Irt and Derwent. It is likely that these last two records are not in the Lake District as defined here.

These localities have not been visited by the present author, who has not recorded *Unio pictorum* and has only one record for *Margaritifera margaritifera*, a small beck flowing into High Borrans Tarn, near Windermere Town.

D. SUMMARY

1. The Lake District is a mountainous area with rocks poor in lime. It is convenient to distinguish; *lakes*, which are the large stretches of water, lying in the main valleys and receiving the water from big drainage areas; *tarns*, which are smaller, in side valleys, and in drainage areas that are much smaller, though large enough to maintain a perennial inflow and outflow; and *pools* which are usually smaller still, shallower, and without perennial outflow.

2. Six species of gastropod, excluding Ancylidae, are common and abundant in Windermere, four are rare and scarce, and one, *Hydrobia jenkinsi*, rare but abundant locally. The common species, *Limnaea pereger*, *Planorbis carinatus*, *P. albus*, *P. contortus*, *Physa fontinalis*, and *Valvata piscinalis*, occur on the stony shore, in reed-beds and in submerged vegetation in deeper water; the last three species occur significantly more often in submerged vegetation than elsewhere. The distribution of *Hydrobia jenkinsi* was mapped in 1937 and again in 1946, when the snail was found to be much scarcer, possibly on account of the erection of an aircraft assembly factory during the war.

3. Lakes can be arranged in a series from Ennerdale, lying in a hard little-weathered, and little-cultivated drainage basin to Esthwaite, lying in softer rocks which, having weathered more, yield more nutrient salts. Settlement on and cultivation of the flat land derived from weathering increases the difference between the lakes. In Ennerdale only *Limnaea pereger* is recorded; in Crummock, another barren 'primitive' lake, *Physa fontinalis* is found as well. In the remaining lakes five of the six species common in Windermere and frequently *Limnaea*

palustris as well are found. *Planorbis carinatus* is known only from Windermere; its arrival is possibly recent. Differences in composition of the snail faunas of the lakes are discussed.

4. Most tarns on the higher fells are glacial in origin, those lower down artificial. The artificial tarns have a richer flora and a rapid succession of plant species. It is convenient to divide this into: stage 1, submerged vegetation; stage 2, floating-leaf stage, in which floating-leaved species cover at least half the tarn; and stage 3, swamp stage, in which *Carex* beds are large and extensive.

5. Estimations of the amount of calcium and the alkalinity show that there may be variation: in different parts of a heavily overgrown tarn; from one inflowing stream to another; and at different times according to the rainfall. The alkalinity fluctuates more than the calcium.

6. Outflow samples from a number of tarns and pools were collected towards the end of uniform spells of weather, a wet spell in winter, a dry spell in winter, a short dry spell in summer, and a long dry spell in summer. Concentrations of calcium and alkalinity were usually, but not invariably, lowest in the winter wet spell and highest in the summer dry spell. The calcium concentration fluctuates most in tarns which have reached stage 3, the swamp stage. The relation between alkalinity and calcium appears to be a factor in snail ecology, though its significance is not understood. Tarns lying to the east of Windermere tend to have a relatively high calcium concentration. All the tarns are characterized by a low calcium concentration, when comparison is made with other parts of the country.

7. Few high natural tarns, few pools, but most artificial tarns harbour snails. A standard collection was made with a pond-net and lasted 60 min. or was converted to numbers caught per hour.

8. Changes in the composition of the population were slight; there were many more snails in most tarns after the war but no reason was apparent; in one tarn, which is omitted from the analyses, there were unaccountable changes in the snail population.

9. *Limnaea pereger* was not found in any of the pools. It was absent from eight out of 40 tarns; five of these had less than 3·0 mg. calcium/l. in the wet winter sample and three were woodland tarns. In a fourth woodland tarn this snail was scarce. In other parts of the country it has been found in lower calcium concentrations.

Planorbis albus occurs most often and in greatest numbers in stage 1 (submerged vegetation) tarns, and becomes scarcer as the tarn becomes overgrown. A high alkalinity relative to calcium is favourable and a low alkalinity relative to calcium unfavourable. Size of the water-body may be important.

Valvata piscinalis, *Physa fontinalis* and *Planorbis contortus* are associated with each other, with *Limnaea palustris*, and with scarcity of *L. pereger* in three tarns. Two are the two largest tarns and the third is peculiar in that rainfall produces a much greater increase in water-level than is usual.

L. palustris is found in tarns which are shown to be 'good' by the study of other groups.

L. glabra is found in a few places where there is thick vegetation and *Sphagnum*. Since such conditions are found widely, the scarcity of *Limnaea glabra* is unaccountable.

L. stagnalis, *Planorbis complanatus*, and *P. crista* are confined to the east side of Windermere, where the general level of calcium concentration is higher, except for one record of *P. crista* to the west of Windermere in Tarn Hows on the Coniston limestone.

P. spirorbis occurs in two lakes and one temporary pool.

Viviparus fasciatus was flourishing in 1948 in a tarn into which it had almost certainly been introduced in 1939.

10. *Ancylastrum fluviatile* occurs in lakes, streams and tarns, almost wherever there is a substratum of rock or stones. *Ancylus lacustris* occurs in Windermere on *Phragmites* stems, and in a quarry pool. The detailed distribution of neither species has been studied.

11. Eleven species of *Pisidium* fall into a 'lake' group and a 'tarn-pool' group, but this is based mainly on shallow-water collections; there is some evidence that 'lake' species occur in the deeper parts of tarns, and two 'tarn-pool' species are the only ones found in the deepest parts of Windermere.

12. Other lamellibranchs recorded are *Sphaerium corneum* and *S. lacustre*, *Unio pictorum* and *Margaritifera margaritifera*.

REFERENCES

Alsterberg, G. (1930). 'Wichtige Züge in der Biologie der Süsswassergastropoden.' Lund.

Boycott, A. E. (1930). 'A re-survey of the fresh-water Mollusca of the parish of Aldenham after ten years with special reference to the effect of drought.' Trans. Herts. Nat. Hist. Soc. Fld Cl. 19: 1–25.

Boycott, A. E. (1936). 'The habitats of fresh-water Mollusca in Britain.' J. Anim. Ecol. 5: 116–86.

Frömming, E. (1936). 'Über den Einfluss der Wasserstoffionenkonzentration auf unsere Süsswasserschnecken.' Int. Rev. Hydrobiol. 33: 25–37.

Frömming, E. (1938). 'Untersuchungen über den Einfluss der Härte des Wohngewässers auf das Vorkommen unser Süsswassermollusken.' Int. Rev. Hydrobiol. 36: 531–61.

Hubendick, B. (1947). 'Die Verbreitungsverhältnisse der limnischen Gastropoden in Südschweden.' Zool. Bidr. Uppsala, 24: 419–559.

Humphries, C. F. (1936). 'An investigation of the profundal and sublittoral fauna of Windermere.' J. Anim. Ecol. 5: 29–52.

Lang, K. (1931). 'Faunistisch-ökologische Untersuchungen in einigen seichten oligotrophen bzw. dystrophen Seen in Südschweden. Acta Univ. Lund. 27 (18): 1–173.

Macan, T. T. (1938). 'Evolution of aquatic habitats with special reference to the distribution of Corixidae.' J. Anim. Ecol. 7: 1–19.

Macan, T. T. (1940). 'Dytiscidae and Haliplidae (Col.) in the Lake District.' Trans. Soc. Brit. Ent. 7: 1–20.

Moon, H. P. (1934). 'An investigation of the littoral region of Windermere.' J. Anim. Ecol. 3: 8–28.

Moon, H. P. (1936). 'The shallow littoral region of a bay at the north-west end of Windermere.' Proc. Zool. Soc. Lond. 491–515.

Oldham, C. (1938). '*Pisidium conventus* in Westmorland and Cumberland.' J. Conch. 21: 51.

Pearsall, W. H. (1921). 'The development of vegetation in the English lakes, considered in relation to the general evolution of glacial lakes and rock basins.' Proc. Roy. Soc. B, 92: 259–84.

Robertson, J. D. (1941). 'The function and metabolism of calcium in the Invertebrata.' Biol. Rev. 16: 106–33.

Standen, R. (1909). 'Notes on the freshwater mussels of Lancashire, and adjacent counties.' Lancs. Nat. 2: 73–6, 105–10.

THE GROWTH AND FOOD OF YOUNG SALMON (*SALMO SALAR*) AND TROUT (*S. TRUTTA*) IN THE RIVER FORSS, CAITHNESS

By WINIFRED E. FROST
Laboratory of the Freshwater Biological Association, Wray Castle, Ambleside, Westmorland

(With 1 Figure in the Text)

1. INTRODUCTION

The River Forss in Caithness, northern Scotland, was chosen as the site for investigation into the life history of the Atlantic salmon (*Salmo salar* L.). Work begun there in May 1939 was suspended in September of that year: during these months I made three visits to the river, 2–4 May, 4–10 June and 20–25 July; on the last two visits collections of young salmon, trout (*Salmo trutta* L.) and invertebrate fauna were made. The fish were examined for age, growth and food to provide data for a comparative study of the two species. Material was collected at two places on the river because it was thought worthwhile to make observations at two slightly different stations. Although results based on two visits are limited it is believed that they are sufficient to justify some conclusions that will be of interest, as there are few comparative studies of salmon and trout in the same waters.

The River Forss (Fig. 1), which is about 26 miles long, lies on Old Red Sandstone (Caithness flagstone series). The upper waters run through peat which overlies the sandstone and at Cnocglass there is, from morainic deposits in the river, evidence of granite. Throughout its course the topography of the river showed little change. At any place the river-bed was usually composed of stretches of coarse sand, coarse gravel and large stones; occasionally there were emergent rocks or flagstones paving the bottom. From Cnocglass to the sea the width of the river was usually about 10–12 m. and there appeared to be little variation in the rate of flow. The surrounding country changed, but not greatly, from the source to the mouth of the river, the upper waters running through peat, the reaches nearer the mouth through pastureland. The upper and lower parts of the river showed some difference in the chemical constitution of the water. It was possible to choose for intensive study of the growth and food of salmon and trout two stations similar in general characteristics but differing somewhat in landscape surroundings and chemistry of the water. The two stations were:

(1) Cnocglass, a place on the upper waters, one of the chief spawning areas of the salmon. Here the river, which is about 10 m. wide and 50 cm. deep, runs through a cutting between peat-covered moraines, the banks being of grass and bracken. The bottom of the river is composed of loose gravel (fist-sized stones and smaller) and of head-sized stones, and in some places there are emergent rocks; all are embedded in coarse sand. Vegetation consisted of patches of *Fontinalis* on the bigger stones and some *Myriophyllum*. The pH ranged from 6·6 to 7·1, the alkalinity as $CaCO_3$ was 49 mg./l., and the conductivity 151 as reciprocal megohms.

(2) Forss Bridge, a place ¼ mile above Forss Bridge and Forss falls, and the lowest reach of the river in which salmon spawn. Here the river, 10–12 m. wide, and about 80 cm. in depth, runs through grazing land and there is no peat. The river bottom is similar to that at the Cnocglass station. The pH ranged from 7·0 to 8·2, the alkalinity as $CaCO_3$ was 81 mg./l., and the conductivity was 208.

The difference between the two stations was slight, but the pastureland surroundings, the higher values for pH, alkalinity and conductivity at Forss Bridge suggest more favourable conditions.

2. MATERIAL AND METHODS

The young salmon collected were fry (0 group) and parr; no smolts were caught, probably because all had migrated by June. The trout were fry (0 group) parr and a few older fish. It is not possible to distinguish, with certainty, the younger stages of brown trout from those of the sea (migratory) trout. It is known that only a few sea trout get above Forss falls, that is to the waters where the fish samples were collected, and therefore it may be presumed that the trout fry and parr were almost entirely those of the brown trout.

The net used for the capture of the fish was designed by Allen (1941). It consisted of a triangular trawl 2·1 m. long with a mouth 1·2 m. high and 2·1 m. wide, to which wings could be attached. The wing attached to one side of the trawl was 1·8 m. long, that to the other 4·6 m., both were 1·2 m. deep. The mouth of the trawl was kept open by corks attached to the head rope and leads on the foot rope,

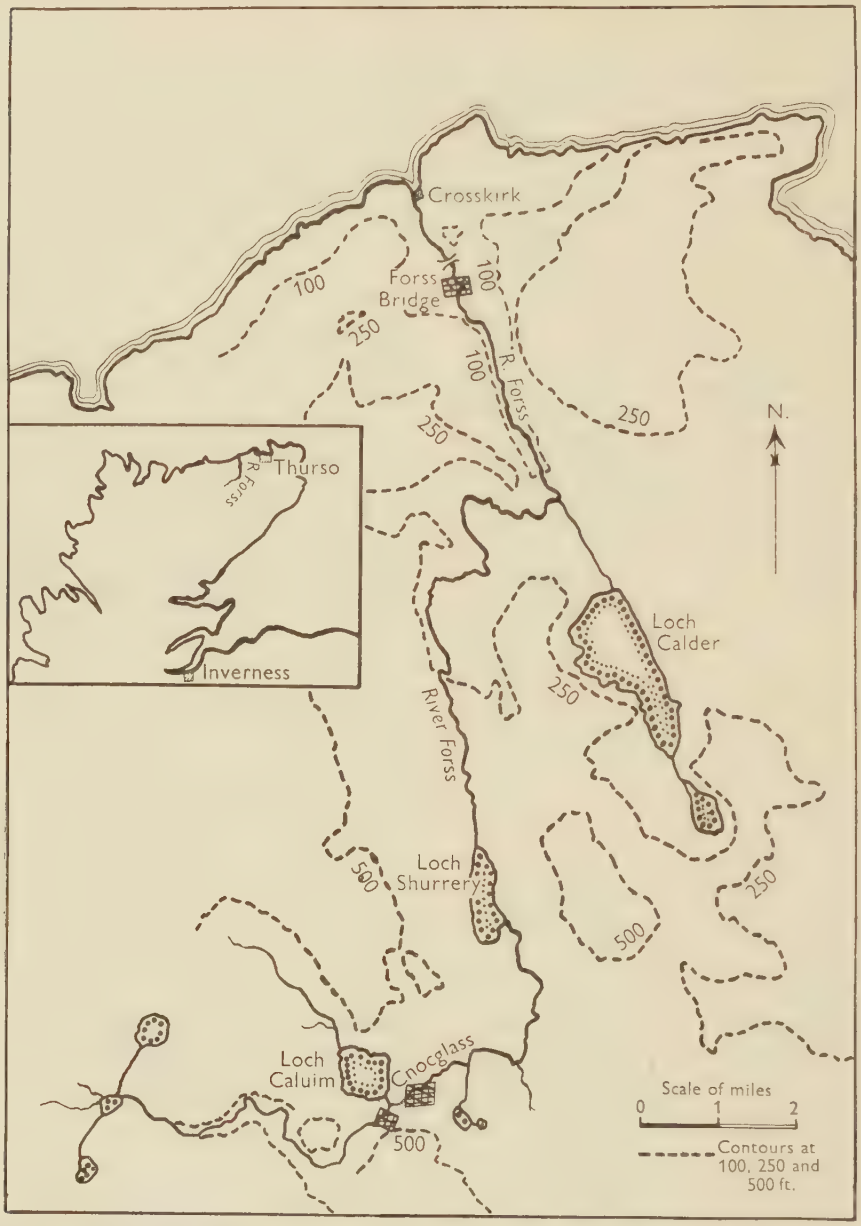


Fig. 1. The course of the River Forss with the position of the observation stations at Cnocglass and Forss Bridge cross-hatched. Inset, northern Scotland showing the position of the River Forss.

and a conical lead weight was attached to the tail of the trawl because it was worked downstream. The wings were also corked and leaded, and the outer ends attached to spreaders. A stop-net, 4·6 m. long, was staked at the end of the reach of river which was to be netted. All nets were of 0·6 cm. (0·25 in.) knot-to-knot cotton netting and the floor of the trawl reinforced with some of stronger kind. The gear was pulled downstream for 75 to 100 m. by two people, one at each spreader, the person on the longer wing on reaching the stop-net brought his wing across the stream and the wings and poke were hauled on to the river bank.

Fish were collected on 6 and 7 June and 21–25 July. In June the river was low and the samples were obtained from three drafts of the net at both Cnocglass and Forss Bridge. In July the river was in flood so that at Cnocglass it was impossible to net

on the June site and nettings had to be made 1 mile farther upstream, and at Forss Bridge it was necessary to make repeated nettings on the June site in order to obtain an adequate sample of fish. It is not possible to say whether or not these variations in sampling technique have affected the results obtained from the material.

In the field each fish was measured to the 0·1 mm. below, from the snout to the fork of tail, weighed to the nearest gram and a sample of scales taken from it. The catch was then preserved in 5% formalin and in the laboratory the sex and state of the gonad was noted. (In some cases fish were returned to the river and the sex could not be noted.)

The age and growth of the fry were known from observation, those of the salmon and trout parr determined from the scales by the method of back calculation. The food of the fish was studied from the examination of the contents of the stomach, namely that part of the gut between the oesophagus and pyloric sphincter. The food organisms were counted individually and identified where possible to the genus. The identification of organisms was done by me, except for the Corixidae and nymphal Plecoptera, which were respectively identified by Dr T. T. Macan and Dr H. B. N. Hynes. The total volume of the food in the stomach was measured and then its dry weight was estimated.

(a) Growth of young salmon and trout

The growth of the fish at the two stations will be considered first, then that of the salmon and trout for the River Forss as a whole.

(1) *Growth at Cnocglass and Forss Bridge*

The growth made by young salmon during the 50 days of 6 June to 25 July 1939 can be deduced from the observed lengths of the fish (Table 2). At Cnocglass the increment was 2·09 cm., at Forss Bridge 1·81 cm. for the salmon fry (0+) and 2·36 and 1·48 cm. at these two places respectively for fish in their second year (1+). There is no statistical difference between growth made at the two places either for fry or parr. These length increments are comparable to those obtained by Allen (1941) for the period June to August on the three tributaries of the River Thurso, a water nearby the River Forss (Fig. 1).

The length attained by the salmon at Cnocglass compared with that at Forss Bridge may be seen from the observed and calculated mean lengths given in Tables 2 and 3. These means, together with their 95% confidence limits, show that only in two instances is there a significant difference in the growth of the salmon at the two stations, namely the June-caught fry (0+) are longer at Forss Bridge than at Cnocglass (Table 2) and the calculated mean length at the end of the first year (Table 3) is greater at Cnocglass than at Forss Bridge.

There are too few parr in their third year (2+) for comment to be made on their growth. Their low numbers suggest that, as on the River Thurso (Allen, 1944), the great majority of the smolts migrate after 2 years.

The growth made by trout in their second year of life (1+) during the 50 days 6 June to 25 July can be found from Table 4, which shows that at Cnocglass the increase was 1·71 cm. and at Forss Bridge 0·73 cm.: there is no statistical difference between the increments at the two places.

The length attained by the trout at Cnocglass compared with that at Forss Bridge may be seen from the observed and calculated mean lengths given

Table 1. *Numbers of young salmon and trout netted in River Forss*

Place ...	Cnocglass			Forss Bridge			Combined stations
Date ...	June	July	June, July	June	July	June, July	June, July
Salmon parr	28	28	56	51	22	73	129
Trout	17	66	83	40	7	47	130
Salmon fry	12	19	31	14	5	19	50
Trout fry	—	19	19	—	13	13	32

3. RESULTS

In Table 1 the number of salmon and trout caught during the investigation is noted; these figures, if they give some indication of the salmonid population, suggest that generally speaking it is much the same at the two stations. The number of salmon and trout together at Cnocglass is of the same order as at Forss Bridge, although the numerical representation of the two fish differs at the two stations. The capture of fry (0+ fish) could be much affected by chance and the numbers taken are unlikely to be representative.

The results of the age and growth studies are given first, then those relating to feeding habits; the number of fish examined for each is given in the appropriate tables.

Table 2. *Number, age, length (cm.) and weight (g.) of salmon of different ages at Cnocglass and Forss Bridge*

	Cnocglass						Forss Bridge					
	June			July			June			July		
Number of fish ...	12	27	1	19	27	1	12	47	4	5	19	3
Age in years ...	0+	1+	2+	0+	1+	2+	0+	1+	2+	0+	1+	2+
Mean length	3·40	9·13	11·80	5·49	11·49	11·10	3·87	9·34	12·45	5·68	10·82	13·50
95 % confidence limits	3·39–3·42	8·84–9·42	—	5·42–5·55	11·14–11·84	—	3·66–4·08	9·05–9·63	—	5·02–6·32	10·37–11·27	—
Standard error	0·01	0·14	—	0·03	0·17	—	0·09	0·15	—	0·23	0·22	—
Mean weight	—	9	20	—	21	15	—	10	24	—	16	31
Range in weight	—	7–12	—	—	13–32	—	—	6–16	20–28	—	8–23	22–37

Table 3. *Mean calculated length (cm.) at the end of each year of life for salmon from Cnocglass and Forss Bridge (number of fish in brackets)*

	Cnocglass (June and July)					Forss Bridge (June and July)				
	Age in years		All fish			Age in years		All fish		
	1	2	Mean length	95 % confidence limits	S.E.	1	2	Mean length	95 % confidence limits	S.E.
Length, end 1st year	6·39 (54)	5·15 (2)	6·34 (56)	6·08 6·60	0·13 —	5·25 (66)	3·60 (7)	5·09 (73)	4·91 5·27	0·09 —
Length, end 2nd year	—	9·95	9·95 (2)	—	—	—	9·84	9·84 (7)	—	—

Table 4. *Number, age, length (cm.) and weight (g.) of trout of different ages at Cnocglass and Forss Bridge*

	Cnocglass							Forss Bridge									
	June		July					June					July				
Number of fish ...	11	2	19	44	11	7	1	5	1	3	2	1	13	4	1	1	1
Age in years ...	1+	2+	0+	1+	2+	3+	4+	1+	2+	3+	4+	5+	0+	1+	2+	3+	4+
Mean length	9·78	15·75	5·91	11·49	15·88	23·10	26·3	12·10	20·00	22·83	27·70	25·0	6·30	12·83	17·40	19·00	23·00
95 % confidence limits	8·97–10·59	—	5·66–6·16	11·03–11·95	15·05–16·71	22·16–24·04	—	10·97–13·23	—	—	—	—	5·94–6·66	10·77–14·89	—	·	—
Standard error	0·37	—	0·12	0·23	0·84	0·94	—	0·48	—	—	—	—	0·17	2·06	—	—	—
Mean weight	12	46	—	19	40	161	—	21	100	127	205	150	—	24	58	70	—
Range in weight	7–18	36–56	—	11–38	23–64	140–196	—	16–28	—	125–130	200–210	—	—	20–31	·	—	—

Table 5. *Mean calculated length (cm.) at the end of each year of life for trout from Cnocglass and Forss Bridge (number of fish in brackets)*

	Cnocglass (June and July)							Forss Bridge (June and July)							
	Age in years				All fish			Age in years					All fish		
	1	2	3	4	Mean length	95 % confidence limits	S.E.	1	2	3	4	5	Mean length	95 % confidence limits	S.E.
Length, end 1st year	5·68 (55)	6·02 (13)	5·61 (7)	6·60 (1)	5·75 (76)	5·47–6·02	0·14	8·42 (9)	8·00 (2)	6·72 (4)	7·63 (3)	6·70 (1)	7·80 (19)	7·16–8·44	0·32
Length, end 2nd year	—	12·30	13·20	15·50	12·77 (21)	11·79–13·68	0·44	—	15·65	14·10	14·60	13·90	14·54 (10)	12·95–16·13	0·71
Length, end 3rd year	—	—	20·59	21·30	20·67 (8)	19·08–22·26	0·68	—	—	19·50	20·10	17·5	19·47 (8)	17·57–21·37	0·81
Length, end 4th year	—	—	—	24·00	24·00 (1)	—	—	—	—	—	24·23	21·1	23·4 (4)	—	—
Length, end 5th year	—	—	—	—	—	—	—	—	—	—	—	23·8	23·8 (1)	—	—

Table 6. *Number, age and length (cm.) of all salmon and trout of different ages from River Forss*

	Salmon						Trout										
	June			July			June						July				
Number of fish ...	24	74	5	24	46	4	0	16	3	3	2	1	32	48	12	8	2
Age in years ...	0+	1+	2+	0+	1+	2+	0+	1+	2+	3+	4+	5+	0+	1+	2+	3+	4+
Mean length	3·64	9·26	12·32	5·53	11·20	12·90	—	10·50	17·17	22·83	27·70	25·0	6·07	11·60	16·00	22·57	24·65
95 % confidence limits	3·50–3·77	9·05–9·47	11·54–13·10	4·35–5·71	10·92–11·48	10·68–15·12	—	9·61–11·39	10·34–24·00	—	—	—	5·87–6·27	11·16–12·03	14·31–17·69	—	—
Standard error	0·07	0·11	0·28	0·09	0·14	0·70	—	0·42	1·59	—	—	—	0·10	0·22	0·77	—	—

Table 7. *Mean calculated length (cm.) at the end of each year of life for all salmon parr and trout from River Forss (number of fish in brackets)*

	Salmon					Trout								
	Age in years		All fish			Age in years					All fish			
	1	2	Mean length	95 % confidence limits	S.E.	1	2	3	4	5	Mean length	95 % confidence limits	S.E.
Length, end 1st year	5·76 (120)	3·91 (9)	5·64 (129)	5·45–5·82	0·09	6·07 (64)	6·28 (15)	6·00 (11)	7·37 (4)	6·70 (1)	6·16 (95)	5·85–6·49	0·15
Length, end 2nd year	—	—	9·86 (9)	8·57–10·14	0·13	—	12·78	13·52	14·82	13·90	13·34 (31)	12·54–14·13	0·40
Length, end 3rd year	—	—	—	—	—	—	—	—	20·40	17·50	20·07 (16)	—	—
Length, end 4th year	—	—	—	—	—	—	—	—	24·17	21·10	23·56 (5)	—	—
Length, end 5th year	—	—	—	—	—	—	—	—	—	23·80	23·80 (1)	—	—

in Tables 4 and 5. These data together with their 95 % confidence limits show that there are only two instances when there is a significant difference in the growth of the trout at the two stations; but both show that growth was better at Forss Bridge than at Cnocglass, namely by the end of the first year of life (Table 5) and during the second year of life (1+) until June (Table 4).

From these observations, it may be concluded in comparing Cnocglass and Forss Bridge with reference to the growth of the two species of fish, that salmon grow better at Forss Bridge until June of the first year, but by the end of the year the fish at Cnocglass exceed in length those at Forss Bridge; there is, however, no difference between the stations that is maintained throughout the parr life. The trout make better growth at Forss Bridge by the end of their first year and until June of their second year, and, although at other times they grow at much the same rate at the two stations, it appears that trout grow somewhat better at Forss Bridge than at Cnocglass.

Comparison of the growth of the two species at the two stations (Tables 2 and 3 compared with Tables 4 and 5) shows that at the end of the first year salmon grow better than trout at Cnocglass but trout grow better than salmon at Forss Bridge. By June in the second year (1+) trout have grown better at both stations and by July trout have grown better than salmon at Forss Bridge. These differences are neither great nor continuous enough to suggest any correlation between them and the difference in the numerical proportions of salmon and trout at the two stations (Table 1).

When the growth of the two species taken together at one station is compared with a similar combination at the other it is found that there is no consistent difference between Cnocglass and Forss Bridge but, because by June of the first (0+) and second (1+) years, growth is better at Forss Bridge it would seem that this station is somewhat more favourable to salmonid fish growth.

From the preceding paragraphs it seems that between the two stations there are no well-defined differences in the growth of the salmon and trout. In view of this the data from the two places may be combined to give a picture of growth of salmon and trout in the Forss as a whole.

(2) *Growth in the River Forss and elsewhere*

The length data from Cnocglass and Forss Bridge combined and their 95 % confidence limits are given in Tables 6 and 7. Significant differences between the growth of salmon and trout show that trout grow better during the fry stage until July, by the end of the first year of life and at the end of the second year of life, from which it may be concluded that, generally speaking, trout grow better than salmon in the River Forss; this conclusion has also been found for the River Liffey (Frost & Went, 1940).

The growth of the salmon and that of the trout in the Forss may be compared with that made by each species in other rivers.

Information, based on young fish, on the growth of salmon in fresh water is available from three rivers, the River Thurso (Allen, 1941) which is near the River Forss, the Eden in northern England (Allen, 1941) and the River Liffey, at Straffan, in Ireland (Frost & Went, 1940). Data from these sources, the logarithmic growth rate for the first and second years of life, the pH and alkalinity of the three waters are given in Table 8.

Comparing the figures for the River Forss with

Table 8. *Comparison of growth of young salmon in different rivers related to values for alkalinity and* pH *of the waters*

Age	River Forss	River Thurso: Sinclair Burn	River Thurso: Sleach Water	River Thurso: Halkirk Burn	River Eden: 1935	River Eden: 1936	River Liffey
			Length in cm.				
June, 1st year	3·64	3·21	3·34	3·85	4·5	4·9	—
July–August, 1st year	5·53	4·13	5·22	6·25	6·5	6·5	—
End 1st year	5·64	4·50	5·90	7·30	7·4	7·4	5·4
June, 2nd year	9·26	6·20	9·1	9·40	10·1	11·1	—
July–August, 2nd year	11·20	8·10	11·15	11·80	12·8	12·6	—
End 2nd year	9·86	8·20	11·50	12·45	13·5	13·7	13·4
			Logarithmic growth rate as percentage per annum				
1st year	81	58	85	107	106	108	77
2nd year	45	40	66	53	60	61	90
Alkalinity as $CaCO_3$ (mg./l.)	49·0–81·0	7·6	22·9	126·0	166·0		158*
pH	6·6– 8·2	6·4	7·1	8·2	8·2		7·9–8·4

* Computed from Frost (1942).

those for the tributaries of the River Thurso it is seen that for the same age the length of the Forss fish is always greater than that of the salmon of the Sinclair Burn, sometimes greater than for the Sleach water and never as great as for the Halkirk Burn. A somewhat similar trend is indicated by the logarithmic growth rate for the first and second years of life. These results suggest that there is a direct correlation between them and the values for alkalinity and pH noted for the three streams and the River Forss. This point is emphasized by the figures for these values for the Eden and Liffey at Straffan (Table 8), for growth in these waters which, like the Halkirk Burn, have a high pH and alkalinity, is in the first or second year or both superior to that in the River Forss.

Growth of the trout in the River Forss cannot be compared with that in the Thurso and Eden as there are no data for these rivers. Comparison may be made with results from Straffan where, as noted, the water is alkaline and from Ballysmuttan, also on the Liffey (Went & Frost, 1942), where the pH is 5·6 and the total hardness at $CaCO_3$ is about 6·7 mg./l. There are no salmon at Ballysmuttan. The growth of the trout in the Forss is at all times much inferior to that at Straffan but it is better than that made at Ballysmuttan. The comparison shows that, as in the salmon, there is a correlation between waters deficient in bases and poor or mediocre growth of the fish and those rich in bases and good growth.

The annual periods of rapid or slow growth of the salmon of the River Forss, as determined from the width of the circuli at the margin of the scales, are similar to those in other rivers. All 79 fish caught in June had widely spaced circuli at the edge of the scale, and of 50 July fish examined 19 (38%) had narrow circuli, 17 of these fish were 1+ and two were 2+ years old. (Jones (1949) who examined scales of 85 young salmon from the River Forss caught in July found only 8% with narrow circuli.) It is concluded from this that in the River Forss growth of the salmon is slowing down in late summer as it does in the Rivers Eden (Allen, 1940), Thurso (Allen, 1941) and Liffey (Frost & Went, 1940).

An annual periodicity of rapid and slow growth was found for the trout of the Forss. In June all the fish (95) had wide circuli at the margins of the scales, in July, of 70 fish, 13 (18·6%) appeared to have narrow circuli at the margin, 12 of these fish were 1+ and one was 3+ years old. These facts suggest that there is an appreciable slowing down of growth towards the end of July; in the River Liffey, because only 5·9% of the July trout had narrow circuli, it would seem that the period of slow growth had not begun markedly by this month in this more southerly river. Thus in the River Forss the periods of rapid and slow growth are at the same time of year for both salmon and trout.

Sexually mature male salmon parr have been found from several rivers by Prof. J. H. Orton and Dr J. W. Jones. In the River Forss, of the 42 males examined by Dr Jones and myself 26 (61·9%) were sexually ripening and three (7%) were probably so. Of these 29 fish, 23 individuals belonged to the 1+ age groups and six to the 2+ age group. This high proportion of ripening males is closely comparable with that in the River Liffey where 74% of the 119 male salmon parr examined were ripening (Frost & Went, 1940).

(*b*) *Food of young salmon and trout*

The stomach contents of 48 salmon fry, 30 trout fry, 83 salmon parr and 74 trout parr were examined. The results are given so that those for June and July, trout and salmon fry, and trout and salmon parr, may be compared (Tables 9–11). The data from the two stations have been combined, because in the absence of some estimate of the invertebrate fauna their comparative value is small.

The food organisms have been arranged in categories which in most cases correspond with a genus or family. The general group 'Coleoptera larvae' was composed chiefly of *Deronectes*; a few dytiscids and *Limnius* were also present. The 'Other Diptera larvae' were tipulids and unnamed species. Adult Ephemeroptera, Plecoptera, Trichoptera and one specimen of *Sialis* have been grouped together. Terrestrial organisms included beetles, aphids, spiders, woodlice, earthworms and winged Diptera. In the tables the number of each kind of food organism is expressed as a percentage of the total organism eaten, while the frequency with which any organism occurred is expressed as a percentage of the total number of fish examined.

The detailed analysis of the food of salmon fry (Table 9) shows that in June, the chief food was chironomid larvae and that *Baëtis* and *Ephemerella ignita* nymphs occurred to an appreciable extent; in July the diet was the same with the addition of nymphal *Centroptilum*. The food of trout fry, examined in July only, was essentially the same as that of the salmon in this month. The summarized data indicate the importance of Ephemeroptera nymphs and chironomid larvae and pupae in the dietary of the fry of salmonids.

The diet of the salmon parr in June (Tables 10 and 11) consisted chiefly of Trichoptera larvae, particularly Limnophilinae, and in July nymphal Ephemeroptera, markedly *Centroptilum* and *Ephemerella ignita*, were the main foods with chironomid larvae eaten to an appreciable extent. The trout in June also fed principally on larval Trichoptera, Limnophilinae

and Leptocerinae; in July the diet consisted of larval Coleoptera and the nymphal Ephemeroptera, *Centroptilum* and *Ephemerella ignita*.

The food consumed by the salmonids was dried and weighed, and the weight expressed as a percentage of the total wet body weight. This figure for salmon in June was 1·43%, in July 1·31%, and for trout in June 0·88% and in July 1·14%. Salmon eat more weight of food than trout in both June and July, and salmon eat more in June than July and trout eat more in July than June. Collectively the figure for salmon is 1·35% and for trout 1·06%.

The food of the young salmon, the trout, and the fry of both species consists essentially of aquatic insect larvae, mainly Trichoptera larvae and Ephemeroptera nymphs and appreciable numbers of larval chironomids and Coleoptera. This diet reflects the character of the invertebrate fauna for random collections, and general observations indicated that aquatic insect larvae were the most abundant

Table 9. *Food of salmon and trout fry in River Forss*

Food organisms expressed as percentage of total organisms eaten (No.) and percentage frequency of occurrence (F.) in total fish examined. Summary, as percentage frequency of occurrence of main food groups, given below. n. = nymph; l. = larva; p. = pupa.

	Salmon				Trout	
Month	June		July		July	
Number of fish	24		23		30	
Mean length in cm.	3·6		5·5		6·1	
Percentage composition ...	No.	F.	No.	F.	No.	F.
Ephemerella ignita (Poda) n.	16·2	25	12·5	52	9·3	48
Baëtis n.	26·1	50	27·0	70	7·3	37
Centroptilum n.	—	—	15·2	22	23·1	37
Caenis n.	0·5	4	—	—	—	—
Ecdyonurus n.	3·1	25	1·3	13	2·4	10
Ephemeroptera n. indet.	—	—	1·8	17	0·8	3
Plecoptera n.	0·5	4	2·2	22	1·2	10
Polycentropidae l.	8·6	42	0·9	9	0·4	3
Hydropsyche l.	—	—	0·5	4	—	—
Hydroptila l.	0·5	4	—	—	1·3	3
Oxyethira l.	—	—	—	—	0·4	3
Trichoptera p.	—	—	0·5	4	0·8	7
Coleoptera l.	2·2	13	1·3	13	8·9	43
Chironomidae l.	38·7	67	34·5	52	25·5	43
Chironomidae p.	0·9	8	0·5	4	12·6	40
Simulium l.	1·8	8	0·9	4	0·4	3
Other Diptera l.	—	—	—	—	0·8	7
Eurycercus lamellatus (Müll.)	—	—	0·9	4	2·4	10
Terrestrial organisms	0·9	8	—	—	2·4	17
Total organisms	222		223		247	

	Salmon		Trout
Summary	June	July	July
Ephemeroptera n.	75	100	96
Plecoptera n.	4	22	10
Trichoptera l.	46	17	13
Coleoptera l.	13	13	43
Chironomidae l. and p.	67	56	63
Simulium l.	8	4	3
Other Diptera l.	—	—	7
Eurycercus lamellatus	—	9	10
Terrestrial organisms	8	—	17

Table 10. *Food of salmon parr and trout in River Forss*

Food organisms expressed as percentage of total eaten (No.) and percentage frequency of occurrence (F.) in total fish examined. n. = nymph; l. = larva; p. = pupa.

	Salmon				Trout				Salmon June, July		Trout June, July	
Month	June		July		June		July					
Number of fish	33		50		17		57		83		74	
Mean length in cm. ...	9·6		11·3		11·4		13·1		10·6		12·6	
Percentage composition	No.	F.	No.	F.	No.	F.	No.	F.	No.	F.	No.	F.
Ephemerella ignita (Poda) n.	4·8	36	21·6	76	—	—	8·4	59	17·2	60	6·9	46
Baëtis n.	4·2	27	11·9	42	1·1	18	0·7	10	9·9	36	0·7	12
Centroptilum n.	2·3	15	37·5	48	—	—	12·1	44	28·3	35	10·0	34
Caenis n.	4·2	30	0·5	8	0·3	6	0·4	9	1·5	17	0·4	8
Ecdyonurus n.	2·1	18	1·7	28	0·3	6	0·3	5	1·8	24	0·3	5
Siphlonurus n.	1·0	6	—	—	1·1	18	0·2	3	0·3	2	0·3	7
Ephemera danica Müll.	—	—	0·2	6	—	—	0·4	10	0·1	4	0·4	8
Leptophlebid n.	0·8	3	—	—	0·3	6	—	—	0·2	1	0·1	1
Ephemeroptera n. indet.	0·8	9	0·3	6	—	—	3·1	18	0·4	7	2·5	13
Plecoptera n.	0·6	6	1·2	22	—	—	0·2	5	1·0	16	0·2	4
Sialis n.	—	—	—	—	—	—	0·3	7	—	—	0·2	5
Polycentropidae l.	6·0	48	0·5	10	2·8	23	0·6	12	1·9	25	1·0	15
Leptocerinae l.	10·0	51	0·9	18	44·2	70	2·4	26	3·3	31	9·7	36
Limnophilinae l.	15·0	42	0·5	10	10·2	65	3·0	24	4·3	23	4·3	34
Hydropsyche l.	4·2	36	0·9	18	2·1	29	0·3	7	1·8	25	0·6	12
Rhyacophila l.	0·6	9	0·2	6	0·8	12	0·2	3	0·3	7	0·2	5
Hydroptila l.	6·0	33	0·1	2	0·8	12	0·1	2	1·6	14	0·2	4
Oxyethira l.	—	—	0·1	2	—	—	—	—	0·1	1	—	—
Lepidostoma l.	1·5	15	0·1	4	1·8	12	0·5	9	0·5	8	0·7	9
Tinodes l.	5·6	21	0·3	6	—	—	—	—	1·7	12	—	—
Trichoptera l. indet.	0·2	3	0·3	6	2·5	23	0·7	16	0·2	5	1·0	17
Trichoptera p.	6·3	40	0·1	2	1·8	6	0·8	12	1·8	17	1·0	11
Coleoptera adult aquat.	0·2	3	0·1	4	1·8	23	0·9	19	0·1	4	1·0	20
Coleoptera l.	10·0	42	3·8	48	0·3	6	28·6	67	5·4	46	23·7	53
Chironomidae l.	4·6	40	7·1	44	6·7	53	7·8	47	6·4	42	7·6	48
Chironomidae p.	2·1	21	2·5	34	1·4	18	4·0	36	2·4	29	3·6	32
Simulium l.	—	—	0·5	10	—	—	0·1	2	0·4	6	0·1	1
Other Diptera l.	—	—	1·4	28	0·3	6	0·5	12	1·0	17	0·5	11
Sigara venusta (Douglas & Scott)	0·6	9	0·1	2	2·1	29	0·3	7	0·2	5	0·6	12
Velia	0·2	3	—	—	—	—	—	—	0·1	1	—	—
Ancylastrum fluviatile (Müll.)	—	—	0·6	10	—	—	0·3	5	0·5	6	0·2	4
Limnea pereger (Müll.)	—	—	0·4	8	—	—	0·7	10	0·3	5	0·6	8
Sphaerium	—	—	—	—	—	—	0·1	2	—	—	0·1	1
Planorbis contortus (L.)	—	—	—	—	—	—	0·6	2	—	—	0·5	1
Gammarus	—	—	—	—	—	—	0·1	2	—	—	0·1	1
Eurycercus lamellatus (Müll.)	0·2	3	1·6	22	—	—	15·6	47	1·2	14	12·9	36
Hydracarina	0·4	6	—	—	—	—	—	—	0·1	2	—	—
Ephem. Plec. Trich. and *Sialis* winged	1·5	18	0·4	12	2·1	35	1·8	23	0·7	14	1·9	26
Terrestrial organisms	4·0	33	2·6	42	15·2	70	3·9	37	3·0	38	5·9	45
Total organisms	520		1465		283		1332		1985		1615	

organisms in the river. Molluscs were poorly represented in both numbers and species and of crustaceans neither *Gammarus* nor *Asellus* was found, the only one noted was the water-flea *Eurycercus lamellatus*.

The diet of the fry of the salmon and trout is almost identical. The numerical representation of Ephemeroptera nymphs, larval Trichoptera and chironomid larvae is much the same, and in many cases the food organisms are of the same genus.

Table 11. *Summary of food of salmon parr and trout in River Forss. Main food groups expressed as percentage frequency of their occurrence in total fish examined (top line)*

	Salmon		Trout		Salmon	Trout
	June	July	June	July	June, July	June, July
	33	50	17	57	83	74
Ephemeroptera nymphs	79	96	47	95	89	84
Plecoptera nymphs	6	22	—	5	16	4
Trichoptera larvae	100	56	95	72	74	77
Coleoptera larvae	42	48	6	67	46	53
Chironomidae larvae and pupae	39	44	12	48	42	39
Aquatic insects misc.	24	30	53	49	27	50
Mollusca	—	14	—	10	8	8
Eurycercus lamellatus (Müll.)	3	22	—	47	14	36
Ephem. Plec. Trich. and *Sialis* winged	18	12	35	23	14	26
Terrestrial organisms	33	42	70	37	38	45

There is no indication that there is a preference for organisms of a small size or belonging to a small species and, although chironomid larvae are more important in the food of fry than of parr, the similarity of the diet of fry and parr is most marked.

The diets of salmon parr and trout are much alike, for in both the chief foods belong to the same faunistic groups: Ephemeroptera, Trichoptera and chironomidae (Table 11). Differences between the two salmonids lie in the extent to which a genus or family of these groups is represented in the diet. There is a broad distinction in diet between the 2 months: in salmon and trout in June, larval Trichoptera are first in importance and nymphal Ephemeroptera second, and in July these conditions are reversed. This distinction between the months is doubtless due to the fact that by late July the numbers and the variety of species of emerging Ephemeroptera nymphs is great and therefore an abundance of easily available nymphs is present for the fish.

In both salmon and trout the majority of the organisms eaten were those which are known to be easily accessible. Coleoptera larvae and *Caenis* nymphs were an exception to this rule, but the former were probably easily available when washed out by the July floods and the latter, because they were almost all ready to emerge as adults, were probably less hidden than normally.

Terrestrial organisms, taken subaqueously or on the surface, were equally important as food to salmon and trout.

Comparison with other rivers shows that on the River Liffey (Frost & Went, 1940) the main foods eaten by salmon parr in June and July were like those eaten by the parr of the River Forss and that the same, generally speaking, is true for the small trout (Frost, 1939). On the Ceirog Brook, a tributary of the Cheshire Dee, salmon parr in June and July ate far more chironomid larvae than Ephemeroptera nymphs (Carpenter, 1940).

4. DISCUSSION

Attention has been drawn by Hartley (1947) to two instances of closely related species of fish sharing the same ecological niche. The trout and salmon of the River Forss provide an outstanding example of this for practically all the habits of the two species are the same. It has been shown that their growth is of the same order, and their diet almost identical. The two salmonids live in the same quickly flowing reaches of the river, have similar spawning grounds and reproductive season. This coincidence of the life histories suggests that interspecific competition is highly probable. It would be expected that this competition would be expressed in the growth of the two fish, particularly in that of the trout, as this species, unlike the salmon, will be subject to the influence of competition throughout its life. Now the River Forss and the River Liffey at Straffan both hold salmon and trout, but the growth of the trout in the Forss is inferior to that of those at Straffan, and it is superior to that of the trout of the Liffey at Ballysmuttan where there are no salmon. It has been pointed out that at Straffan the waters are hard and have a high pH, and that at Ballysmuttan they are soft and have a low pH—characteristics in which the River Forss is appreciably more like Ballysmuttan than Straffan. In view of this evidence it would seem that the relatively poor growth of the trout in the River Forss is more likely to be due to the base-deficient character of the water than to be an expression of competition between salmon and trout. There are no data for a comparison of the growth of trout in a river rich in bases and holding salmon and trout, with the growth made in a similar water but containing trout only. It may be suggested, however, that, under such circumstances, if it were found that the growth of the trout in the salmon-trout river were not so good as in the salmon-free

river, then the slower growth might be attributed to interspecific competition.

Thus, as it seems unlikely that interspecific competition is the primary cause of poor growth of brown trout in acid base-deficient waters, it is questionable if, as a conservation measure for a salmon-trout river of this type, elimination of the salmon would result in improved growth of the trout.

5. ACKNOWLEDGEMENTS

I am much indebted to my colleagues Dr T. T. Macan and Mr E. D. Le Cren for their helpful criticism of the manuscript, and to Dr C. H. Mortimer for the water analyses of the Forss.

6. SUMMARY

1. The growth and food of young salmon (*Salmo salar* L.) and trout (*S. trutta* L.) in the River Forss, northern Scotland were investigated from material collected in June and July 1939.

2. Investigations were carried out at two stations, Cnocglass on the moorland reaches with a pH of 6·6–7·1 and alkalinity as $CaCO_3$ 49 mg./l. and at Forss Bridge on the lower reaches, where the pH was 7·0–8·2, and alkalinity as $CaCO_3$ was 81 mg./l.

3. Although various comparisons of the growth of salmon and trout show that there are slight differences between growth made at Cnocglass and Forss Bridge there is no indication of a well-defined difference in the growth at the two stations of either species.

4. When the stations are ignored it is found that in the River Forss as a whole trout grow better than salmon.

5. Results from the two stations combined show that the diet of the salmon and trout consisted essentially of aquatic insect larvae.

6. The food of the fry of both salmonids was mainly Ephemeroptera nymphs and larval and pupal chironomidae and the chief foods of salmon parr and trout were Trichoptera larvae and nymphal Ephemeroptera. Some differences in the diet of June and July were noted.

7. The identity of growth rate, feeding and other habits of young salmon and trout probably result in interspecific competition. The relationship between this and the growth of trout is discussed.

REFERENCES

Allen, K. R. (1940). 'Studies on the biology of the early stages of the salmon (*Salmo salar*). 1. Growth in the River Eden.' J. Anim. Ecol. 9: 1–23.

Allen, K. R. (1941). 'Studies on the biology of the early stages of the salmon (*Salmo salar*). 3. Growth in the Thurso River system, Caithness.' J. Anim. Ecol. 10: 273–95.

Allen, K. R. (1944). 'Studies on the biology of the early stages of the salmon (*Salmo salar*). 4. The smolt migration in the Thurso River in 1938.' J. Anim. Ecol. 13: 63–85.

Carpenter, K. E. (1940). 'The feeding of salmon parr in the Cheshire Dee.' Proc. Zool. Soc. Lond. A, 110: 81–96.

Frost, W. E. (1939). 'River Liffey Survey—II. The food consumed by the brown trout (*Salmo trutta* Linn.) in acid and alkaline waters.' Proc. R. Irish Acad. 45 B: 139–206.

Frost, W. E. (1942). 'R. Liffey Survey IV. The fauna of the submerged "mosses" in an acid and an alkaline water.' Proc. R. Irish Acad. 47 B: 293–369.

Frost, W. E. & Went, A. E. J. (1940). 'River Liffey Survey—III. The growth and food of young salmon.' Proc. R. Irish Acad. 46 B: 53–80.

Hartley, P. H. T. (1947). 'The natural history of some British freshwater fishes.' Proc. Zool. Soc. Lond. 117: 129–206.

Jones, J. W. (1949). 'Studies of the scales of young salmon *Salmo salar* L. (juv.) in relation to growth, migration and spawning.' Fish. Invest. Ser. 1, 5, no. 1: 23 pp.

Went, A. E. J. & Frost, W. E. (1942). 'River Liffey Survey. V. Growth of brown trout (*Salmo trutta* L.) in alkaline and acid waters.' Proc. R. Irish Acad. 48 B: 67–84.

A FURTHER ECOLOGICAL STUDY OF THE RIVER RHEIDOL: THE FOOD OF THE COMMON INSECTS OF THE MAIN-STREAM

By J. R. ERICHSEN JONES

Department of Zoology, University College of Wales, Aberystwyth

(With 2 Figures in the Text)

CONTENTS

	PAGE		PAGE
1. Introduction	159	7. The Trichoptera	167
2. The conditions of existence	159	8. The Coleoptera	169
3. The available supply of vegetable food	160	9. Other insects	169
4. Literature and technique	163	10. General observations	170
5. The Plecoptera	163	11. Summary	174
6. The Ephemeroptera	166	References	174

1. INTRODUCTION

The Rheidol, which flows into Cardigan Bay, is a good example of a swift, stony river of medium size. A number of papers have appeared, dealing with its history of pollution (Carpenter, 1924, 1925; Laurie & Jones, 1938; Newton, 1944), and recently the writer (1949*a*) has published a general account of the river describing the fauna of the main-stream and the backwaters, together with physiographical data. The present paper deals with the feeding habits of the characteristic insect species of the main-stream and is based on the examination of the gut contents of about 1300 specimens.

2. THE CONDITIONS OF EXISTENCE

The general environmental conditions of the fauna have been discussed in the earlier study (Jones, 1949*a*, pp. 67–78) and may be summarized as follows. The main-stream has a total fall of about 1750 ft., a length of about 28 miles and is for the most part about 100 ft. in width. The river draws most of its water from peaty land over 1000 ft. in altitude—the west and north-west slopes of Plynlimmon, and throughout its course, in many respects, has the general character of a large mountain stream. The water is very soft and acid, its pH varying from 6·4 at low level to 5·8 at full flood. The current is swift, exceeding 5 ft./sec. on the riffles even when the level of the river is low. Floods are frequent and violent; at full flood the level of the river, near Aberystwyth, rises about 2 ft. and the mid-stream current is nearly 6 ft./sec. In its upper reaches the stream-bed is largely rocky; in its lower reaches the bed is composed of pebbles and gravel and is very unstable so that the course of the river is continually changing. The river water is well oxygenated, but its turbulence permits only a small degree of supersaturation; the highest oxygen concentration recorded, on a sunny, spring day when the river bed was covered with green algal growth, is only 101·8%. Temperature conditions are favourable; the river rarely freezes and on cool, sunny days the water may be 2–3° C. warmer than the air. After many days of hot sunshine, however, the water temperature does not exceed 22° C.

In 1931–2, when the faunistic survey of Laurie & Jones (1938) was made, the river was still very slightly polluted with lead, carrying about 0·1 mg. Pb/l. in solution at full flood and 0·02–0·03 mg./l. at normal or low level. At this time there was no evidence that the pollution limited the invertebrate fauna to any degree, and during the last 17 years there has been at least no deterioration in the river's chemical condition; it has now been stocked with trout and the fishing is protected. There is no appreciable amount of sewage pollution, for its valley is thinly inhabited.

The insects of the river have few enemies apart from predatory members of their own group, the trout (*Salmo trutta*) and Hydracarina. Leeches are very rare in the main-stream and there are no large Crustacea. Newts are extremely rare; the stickleback (*Gasterosteus aculeatus*) occurs in fair numbers in the lower reaches of the river, mainly in the backwaters, but there are no other insectivorous fish such as the loach, gudgeon or bullhead, and eels are

rare. Prior to the summer of 1949 minnows (*Phoxinus phoxinus*) were conspicuous by their absence, but in June 1949 small numbers appeared in the *Ranunculus* beds near Penybont. This addition to the fauna of the river is a further indication of its present freedom from pollution.

3. THE AVAILABLE SUPPLY OF VEGETABLE FOOD

The available supply of vegetable food may be classified into: (1) the macroflora—bryophytes and flowering plants growing in the water; (2) the algae or microflora; (3) detritus; and (4) plant material originating outside the river.

On the rocky bed in the upper and middle reaches of the river there is a fair growth of moss (*Fontinalis antipyretica* L.) and at some points, principally in rock pools in the gorge section, a liverwort (*Aplozia crenulata* Sm.) is common; but in its lower reaches the stony main-stream is for the most part destitute of bryophyte growth. It is probable that the instability of the river-bed is an obstacle, for where there are firmly fixed rough stones (around the foundations of the bridges) *Fontinalis* grows in abundance. *Ranunculus fluitans* and *Callitriche* sp. occur in the main-stream at points where the current is moderate and there are deposits of sand, and *Glyceria fluitans* is fairly common near Aberystwyth. Generally speaking, however, the macroflora of the river is poor, and for most of its course the main-stream has a bare and monotonous stony bed, with no plants other than the algae.

An account of the microflora of the river, with quantitative data for 1934 and 1935, has been given by Reese (1937); this refers mainly to its upper and middle reaches, stations B and D in the writer's survey (Jones, 1949*a*). The following notes on the microflora are based on Reese's data and observations made by the writer between February 1948 and July 1949.

Stigeoclonium falklandicum Kütz. is the dominant green alga throughout the course of the main-stream and occasionally appears in such abundance as to cover the river-bed with green growth. Other filamentous Chlorophyceae which occur from time to time are *Ulothrix*, *Microspora*, *Mougeotia*, *Draparnaldia*, *Zygnaema* and *Spirogyra*, but these never seem to rival the *Stigeoclonium* in abundance and are generally somewhat rare. The Chlorococcales are represented by *Ankistrodesmus falcatus* (Corda) Ralfs, *Selenastrum gracile* Reinsch, *Tetraëdron minimum* (A. Br.) Hansg. and *Scenedesmus obliquus* (Turp.) Kütz., but none is common.

A small species of *Closterium* (*C. subulatum* (Kütz.) Bréb.) is abundant in the main-stream in spring and early summer, on the stones of the stream-bed and among the leaves of macrophytes, but otherwise the desmids are rather rare. Species recorded include *Closterium Ehrenbergii* Menegh., *C. acerosum* (Schrank) Ehrenb. and *C. acutum* (Lyngb.) Bréb., *Euastrum binale* (Turp.) Ehrenb., *Cosmarium reniforme* (Ralfs) Arch., *Penium cucurbitinum* Biss, *Staurastrum polytrichum* Perty and *S. Kjellmani* Wille, *Arthrodesmus Incus* (Bréb.) Hass. and *A. octocornis* Ehrenb., *Gonatozygon monotaenium* De Bary, *Spondylosium papillosum* W. & G. S. West and *Hyalotheca dissiliens* (Sm.) Bréb. Desmids are named according to the monograph of W. and G. S. West (1904–23), the nomenclature of other algae follows Smith (1933).

The blue-green algae are represented chiefly by *Phormidium* and the Chamaesiphonales. Reese (1937, p. 405) recorded three abundant species—*Phormidium tenue* (Menegh.) Gom., *Chamaesiphon incrustans* Grun. and *Chamaesiphonopsis regularis* Fritsch; other blue-green algae are rare. Two species of Rhodophyceae—*Batrachospermum moniliforme* Roth and *Lemanea* (*Sacheria*) *mammillosa* Kütz. are common at all parts of the main-stream, particularly in winter and early spring. These 'red' algae grew in the river when it was heavily polluted with lead and almost destitute of plant life (Carpenter, 1924, p. 2) and, as will be shown later, they figure largely in the diet of some of the river's most abundant animals.

The diatoms are represented by about fifty-six species. These are listed in Table 1, roughly classified in four orders of abundance. This list is based on ten samples taken from the lower reaches of the main-stream during the period October 1948–June 1949. During the winter *Tabellaria flocculosa* is generally the dominant species, but in spring and summer it may be surpassed in numbers by *Achnanthes minutissima*, *Meridion circulare* and *Gomphonema parvulum*. *Achnanthes* tends to be a dominant form on the pebbles, while *Meridion* and *Gomphonema* are abundant among the macrophytes. Some collections were made in the upper reaches of the river at station B (see Jones, 1949*a*, Fig. 1 for the location of collecting stations) in May and June 1949; nearly all the species listed in Table 1 were represented, and *Tabellaria flocculosa*, *Asterionella formosa*, *Eunotia arcus* and *Frustulia rhomboides* seemed to be rather more abundant than in the samples taken near Aberystwyth. For identification the diatom samples were treated with nitric acid, washed in the usual way and mounted preparations were made with Gurr's 'Clearax'.

The quantitative data for the River Tees given by Butcher, Longwell & Pentelow (1937) indicate that the microflora of swift, stony rivers, in which floods are frequent, undergoes violent and irregular variation in density. All types of algal growth are not

Table 1. *Diatoms collected in the lower reaches of the main-stream of the Rheidol, October 1948–June 1949*

The nomenclature is that of Hustedt, 1930

(1) The dominant species, present in all samples and usually abundant

Tabellaria flocculosa (Roth) Kütz.
Achnanthes minutissima Kütz. var. cryptocephala Grun.
Gomphonema parvulum (Kütz.) Grun.

(2) Sub-dominant species, occasionally abundant

Meridion circulare Ag. var. constricta (Ralfs) van Heurck
Diatoma hiemale var. mesodon (Ehr.) Grun.
Achnanthes microcephala Kütz.
Gomphonema angustatum (Kütz.) Rabh.

(3) Common; present in most samples in fair numbers

Fragilaria capucina Desmaz.
Eunotia lunaris (Ehr.) Grun.
Achnanthes linearis W. Smith.
Navicula Rotaeana (Rabh.) Grun.
Surirella ovata Kütz.
Pinnularia interrupta W. Smith

(4) Rare

Cyclotella sp.
Tabellaria fenestrata (Lyngb.) Kütz.
Meridion circulare Ag.
Ceratoneis arcus Kütz.
Fragilaria virescens Ralfs
F. undata W. Smith
Asterionella formosa Hassall
Synedra ulna (Nitzsch) Ehr.
S. acus Kütz.?
Eunotia pectinalis (Kütz.) Rabh.
E. pectinalis var. ventralis (Ehr.) Hust.
E. arcus Ehr. var. fallax Hust.
E. tridentula Ehr. var. perminuta Grun.
E. monodon Ehr. var. major (W. Smith) Hust.
E. praerupta Ehr.
Cocconeis placentula Ehr.
Achnanthes lanceolata Bréb.
Frustulia rhomboides (Ehr.) de Toni
F. vulgaris Thwaites
Gyrosigma acuminatum (Kütz.) Rabh.
Neidium iridis (Ehr.) Cleve fo. vernalis Reichelt
N. iridis var. amphigomphus (Ehr.) van Heurck
N. affine (Ehr.) Cleve
Stauroneis phoenicenteron Ehr.
Navicula rhyncocephala Kütz.
N. viridula Kütz.
N. gracilis Ehr.
Pinnularia borealis Ehr.
P. gibba Ehr.
P. viridis (Nitzsch) Ehr.
P. maior (Kütz.) Cleve
Amphora ovalis Kütz.
Cymbella cuspidata Kütz.
C. ventricosa Kütz.
C. sinuata Greg.
C. affinis Kütz.
C. cistula (Hempr.) Grun.
Gomphonema acuminatum Ehr.
G. acuminatum var. coronatum (Ehr.) W. Smith
G. gracile Ehr.
G. lanceolatum Ehr.
G. constrictum Ehr.
Nitzschia palea (Kütz.) W. Smith
N. acicularis W. Smith
N. linearis W. Smith
Surirella biseriata Bréb.

affected by floods to the same extent; encrusting forms like *Chamaesiphonopsis* and *Chamaesiphon* can survive very swift currents; the diatoms, which are insecurely attached, are swept away. Thus Reese (1937, p. 399) has recorded that a diatom population of 702/sq.mm. was reduced to 44/sq.mm. by flooding. The violent fluctuations that occur in the diatom population of the Rheidol are readily perceived; after a period of dry, sunny weather an abundant brown growth will develop on the pebbles in shallow water near the margins of the flood-beaches and may extend to cover almost the whole of the river-bed; a heavy flood will sweep all this away to leave the stones clean and grey. Generally speaking the microflora, particularly the diatoms, would appear to form a somewhat unreliable source of food at all seasons of the year.

A more reliable source of food is detritus—amorphous organic matter formed mainly by the disintegration and decay of plants. This accumulates among the stones and gravel of the stream-bed and is strained out of the flowing water by the phanerogams. Some of it is formed by the disintegration of vegetation growing in the water, some of it has its origin outside the river for much decaying terrestrial plant material must be washed into the river by rain. Whatever its source, it would appear that adequate supplies are always available, probably a maximum amount in late autumn and early winter.

Much of the valley of the Rheidol is well wooded, and great quantities of dead leaves find their way into the river to be deposited at the bottom of pools or trapped between stones on the riffles. Under the large stones in swiftly flowing water considerable

accumulations of oak and elm leaves can be found during the winter. These form an important source of food: some insects feed on them by biting off pieces, others apparently swallow the fragments into which they are eventually broken by the grinding action of the stones and gravel. No other plant material growing outside the river appears to form a major food source except in so far as it contributes to the general supply of detritus.

4. LITERATURE AND TECHNIQUE

A brief review of the literature dealing with the feeding habits of aquatic insects is given in my paper dealing with the ecology of the River Sawdde (Jones, 1949*b*, pp. 151–2) and some additional works are referred to in the course of this paper. The methods adopted for the determination of the gut contents of specimens from the Rheidol followed closely those adopted in the work on the Sawdde fauna; to aid in the accurate identification of the prey of predatory species a comprehensive series of balsam slides was prepared illustrating the mouthparts, legs, gill lamellae, etc., of all the common insects of the main-stream and additional temporary preparations were made as required. Most of the material for examination was collected from the lower reaches of the river, near Aberystwyth; this could be transported to the laboratory very quickly and examination of the gut contents could be begun within 30 min. Speedy examination is advisable when plant material has to be identified; the chloroplasts of algae are quickly digested. Insect food is digested much more slowly and can be identified even if the specimen to be examined is kept alive in the laboratory for some hours before its gut is extracted.

In the case of the Ephemeroptera and Plecoptera, when specimens were picked out for examination, care was taken to avoid mature nymphs about to moult to the winged stage, for these almost invariably have the gut quite empty. Such cases are readily distinguished by the size and dark colour of the wing buds. Otherwise specimens were taken at random from the material collected.

In Tables 2–5, which summarize the results, *all figures*, except the number of specimens examined and their size range, are *percentages*, and indicate the percentages of the specimens examined in which the different 'foods' were found, the percentages which contained digested food only, and so on.

The presence of algae is indicated only when some, at least, of the cells contained chloroplasts, showing that the insect had been feeding on the living plant, and diatoms are indicated as present only when the gut contained what appeared to be a substantial number. Odd diatoms were present in most of the specimens examined, many are sometimes seen in the gut of predatory insects and these are usually part of the food of the prey. Many specimens contained plant material broken up into very small pieces; when these pieces were clearly of a cellular nature the gut contents were recorded as including 'fragmented leaf and stem tissue'. What appeared to be vegetable matter broken down into an amorphous mass mixed with grit is recorded as 'detritus'. It will be understood that the distinction between detritus and partially digested plant food of other types is frequently difficult. True detritus, however, always appears to include a considerable proportion of grit.

5. THE PLECOPTERA

The observations on the Plecoptera are summarized in Table 2. It will be noted that *Perlodes** is mainly carnivorous, *Isoperla* and *Chloroperla* are omnivorous, while *Leuctra*, *Protonemura* and *Amphinemura* subsist almost entirely on vegetable food. During autumn and winter *Perlodes* is the dominant predatory insect in the river and is a most voracious animal; the crop in a large specimen measures about 9 by 2·5 mm. and in the majority of cases is fully distended with food. Usually the meal consists of a comparatively small number of insects of large size; 84 of the nymphs contained animal food totalling approximately 257 prey individuals, an average of about three per specimen. The *Leuctra* nymphs were mainly found in the specimens taken from the upper reaches of the river (station B); *Baëtis* and *Rhithrogena* were the chief prey in those captured near Aberystwyth. The smallest *Perlodes* examined measured about 10 mm., the diet of these specimens did not appear to differ from that of the large ones in any important respect; the prey tended to consist of smaller specimens of the same species.

Like *Perla* and *Dinocras*, *Perlodes* swallows its prey entire, and in a suitable running-water apparatus will feed in the laboratory. Small *Baetis* nymphs are seized and disappear from sight in a few seconds, but the consumption of a large *Rhithrogena* takes some time. The *Perlodes* seizes the *Rhithrogena* with a swift rushing movement, generally by the posterior end of the body and about one-third of the prey is swallowed immediately; then there is a pause during which the stonefly stops quite still or walks about with the captured insect protruding from its mouth. After a short time swallowing recommences; the mandibles and maxillae work to and fro gently gripping the mayfly nymph and drawing it into the throat. Several minutes after capture the prey disappears from sight, its mouthparts still moving feebly.

* All generic and specific names of British insects in this paper follow the check-list of Kloet & Hincks (1945).

Table 2. *Summary of observations on the gut contents of the plecopteran nymphs*

Explanation in the text, § 4

Species ...	*Perlodes mortoni* (Klap.)	*Isoperla grammatica* (Poda)	*Chloroperla tripunctata* (Scop.)	*Leuctra hippopus* Kemp.	*Protonemura meyeri* (Pict.)	*Amphinemura cinerea* (Oliv.)
Number of specimens examined	100	100	120	50	50	80
Size range (mm.)	10–25	6–12	4–9	6–8	6–8	3–6
Months	Oct.–Mar.	Jan.–Apr.	Nov.–Apr.	Feb.–Apr.	Nov.–Mar.	Feb.–Apr.
Collection stations	B, C, D, E	E	D, E	D, E	D, E	D, E
Anterior part of the gut empty	6	8	1	16	4	15
Gut contents digested	7	5	6	14	14	22
Gut contents:						
Detritus	4	2	33	62	34	38
Moss fragments (*Fontinalis*)	—	—	3	8	12	2
Other fragmented leaf and stem tissue	3	5	30	36	60	35
Algae						
Green algae						
Ulothrix	—	—	2	—	—	—
Microspora	—	1	4	2	8	1
Stigeoclonium	2	1	5	—	18	1
Mougeotia	—		1		2	
Pleurotaenium	—	—	1	—	-	—
Closterium	—		4	—	2	—
Cosmarium	—		2	-	2	—
Gymnozyga	—	.	1	—	—	—
Green algae not identified	4	2	4	4	10	2
Lemanea	4	15	12	—	—	2
Batrachospermum	...	10	30	2	4	4
Diatoms	2	3	40	4	6	6
Phormidium		—	1	—	—	—
Rotifera		—	—	—	—	1
Oligochaeta		3	10	—	—	—
Copepoda						
Cyclops sp.	—	—	1		—	—
Cladocera	—	—	1	—	.	—
Hydracarina	—	—	1	-		—
Plecoptera (nymphs)						
Isoperla	1	1	—	—		—
Chloroperla	6	8	-	-	-	—
Leuctra	19	3	3		.	
Protonemura	1	—	—		—	- -
Amphinemura	1	—	—		. .	- -
Not identified	—	1	—		—	—
Ephemeroptera (nymphs)						
Baëtis	32	18	18	—	—	1
Rhithrogena	27	22	7	—	—	—
Ecdyonuridae not determined	11	1	—	-	--	—
Odonata (naiads)						
Ischnura (?)	1	—	—	—		—
Cordulegaster	1	—				—
Trichoptera (larvae)						
Polycentropus	3	1	—			-
Hydropsyche	5	—	—			-
Limnophilidae	2	—	—			—
Coleoptera (larvae)						
Dytiscidae	3	—	-	-	.	-
Elminae	1	—	—	—	—	—

Table 2 (*continued*)

DIPTERA (larvae)						
Limnophila	—	1	—	—	—	—
Dicranota	—	—	1	—	—	—
Simulium	24	—	—	—	—	—
Chironomidae	10	30	12	—	—	—
DIPTERA (pupae)						
Simulium	1	—	—	—	—	—
Remains not identified	4	2	2	—	—	—
Animal food only	77	58	17	—	—	—
Animal and vegetable food	7	13	32	—	—	2
Vegetable food only	3	14	44	70	82	61
Anterior part of the gut empty, with its contents digested or with none of the contents identified	13	15	7	30	18	37

Isoperla appears to be more partial to plant food than *Perlodes*, for a number of the specimens contained masses of *Batrachospermum* and *Lemanea*, and the prey organisms tend to be smaller; chironomid larvae form a very large part of the diet, fifty prey individuals being found in the 100 nymphs examined, and there appears to be some tendency for the nymphs to become more carnivorous as they increase in size; fifty-five 6 mm. specimens were examined in January and February, of these forty-seven contained food and this was entirely animal in twenty-four cases; of the thirty 9–12 mm. specimens examined in April twenty-six contained food and this was entirely animal in twenty-four.

Chloroperla tripunctata is another abundant form during autumn, winter and spring. *C. torrentium* occurs also but is much less common. An important feature of the diet of the species studied is its great variety; almost any form of plant food is eaten, and in addition small nymphs of *Baëtis*, *Rhithrogena* and *Leuctra*, chironomid larvae and oligochaetes. Many specimens contained a substantial number of large diatoms such as *Pinnularia viridis* and *Surirella biseriata*. No significant difference was noted between the diet of 4–5 mm. nymphs examined in November and large specimens taken from the river in April.

Of the four species of *Leuctra* occurring in the Rheidol (*fusciventris* Steph., *inermis* Kemp., *nigra* Oliv. and *hippopus* Kemp.) the last is the most common and this species was chosen for study. In a typical 7 mm. specimen the 'stomach' is about 4 mm. in length; the anterior third usually contains a mass of finely divided plant material mixed with gritty detritus. It would appear that the vegetable matter is speedily digested and the mineral matter accumulates in the gut, the posterior third of which is usually packed with grit and little else. *Leuctra* does not seem to eat *Batrachospermum* or *Lemanea* even when there is an ample supply, and when *Chloroperla* nymphs collected from the same part of the river-bed, on the same occasion, have their crops filled with these algae.

Protonemura seems to have a more varied diet than *Leuctra*, but subsists mainly on leaves. Some variety of leaf tissue was seen in the specimens examined; in those taken from stones on the riffles the leaf fragments were very dark, bore numerous stellate hairs and were evidently pieces of dead leaves of deciduous trees. Fragments of moss were also seen and nymphs taken from vegetation at the margins of the river frequently had the gut filled with yellow and green pieces of *Glyceria*. The diet of *Amphinemura* is similar, but fewer specimens had fed on green algae.

In general, these observations on the Plecoptera are in agreement with those of Hynes (1941) who has studied the feeding habits of all the British species of this order. Hynes states, however, that usually from about 50 to 90% of the specimens he examined had no food in their alimentary canals (1941, p. 532). Table 2 shows that in the case of the Rheidol specimens the proportion which contained no food was much lower than this. Even in the case of *Amphinemura cinerea*, the species in which the greatest number of cases with no food occurred, the proportion of those which had recognizable food material in the anterior part of the gut always exceeded 50% and in the case of *Perlodes* about 80% of the specimens examined had taken an ample meal. Whether this indicates that in the Rheidol there is less competition for the food supply available cannot be decided without further investigation.

Grau (1926) examined the gut contents of a number of plecopteran nymphs including *Perlodes dispar* Rmb., which was found to feed mainly on Ephemerid nymphs, chironomid larvae and *Gammarus*. Frison (1929, 1935) has discussed the feeding habits of the nymphs of North American species of Plecoptera; he concludes that in Illinois all the fall and winter stoneflies are herbivorous (1935, p. 301)

and that the carnivorous Perlidae comprise a group of species essentially belonging to the late spring and early summer. This seems a curious reversal of the conditions in the Rheidol where the carnivorous species are predominant during the winter. The chief predatory British species of Plecoptera whose nymphs occur during the summer are *Dinocras cephalotes* (Curt.) and *Perla carlukiana* Klap., but these do not occur in the Rheidol. The reasons for their absence are not understood. According to Hynes (1941, p. 529, Fig. 19) *Dinocras* (*Perla cephalotes* in Hynes's nomenclature) likes stony rivers with a stable substratum while *Perla carlukiana* is common in rivers in which the bottom is unstable. Both species occur in smaller streams and over a wide altitude range. *P. carlukiana* occurs in the Towy, the Teifi and the Dovey, all larger rivers than the Rheidol but with less acid water.

Table 3. *The Ephemeroptera*

Species ...	*Ephemerella notata* Eaton	*Baëtis rhodani* (Pict.)	*Siphlonurus lacustris* Eaton	*Rhithrogena semicolorata* (Curt.)	*Heptagenia lateralis* (Curt.)
Number of specimens examined	40	80	40	50	30
Size range (mm.)	5–10	6–10	8–14	7–13	3–7
Months	June	Jan.–Mar.	Apr.–May	Jan.–Mar.	Mar.–Apr.
Collection station	E	E	E	E	E
Anterior part of the gut empty	5	2	2	2	7
Gut contents digested	—	8	15	6	20
Gut contents:					
Detritus	82	86	75	92	73
Fragmented leaf and stem tissue	17	2	72	8	7
Algae					
Green algae					
Stigeoclonium	60	—	2	—	—
Spirogyra	2	—	—	—	—
Closterium	35	—	—	—	—
Cosmarium, Staurastrum and other desmids	5	—	12	—	—
Batrachospermum (including Chantransia stage)	—	43	—	4	—
Diatoms	55	16	13	4	10
Algae not identified	—	—	5	6	—
Other material not identified	—	—	—	1	—

6. THE EPHEMEROPTERA

The observations on the Ephemeroptera are summarized in Table 3. As in the case of the Plecoptera each species was studied during that period of the year when large numbers of nymphs of moderate to large size could be collected; *Baëtis rhodani* occurs in fair numbers in most months of the year, the others have fairly definite seasons (see Jones, 1949*a*, p. 85).

Rhithrogena and *Heptagenia* are essentially detritus feeders, and in typical cases the anterior part of the gut contains a smooth mass of amorphous matter and grit. In this some very small leaf fragments, pieces of *Batrachospermum*, or a few diatoms may be seen, but the relative amount of such matter is always small. As in the case of *Leuctra* the organic matter appears to be digested quickly and the mineral matter accumulates at the posterior end of the gut, which is usually packed with a mass of grit; this sometimes contains so little organic matter as to appear very light coloured. Unlike *Ecdyonurus*, which lives near the margins of streams and thus seems to escape the predatory Plecoptera (Jones, 1949*b*, p. 156), *Rhithrogena* likes fairly deep water and a swift current; hence it is preyed upon by *Perlodes*. *Heptagenia* appears later in the year than *Rhithrogena*, after *Perlodes* has bred out, and does not seem to have any stonefly enemy.

Baëtis also seems to subsist mainly on detritus, but a high proportion of the specimens examined contained a considerable amount of *Batrachospermum*. In the nymphs collected in January and February numerous small pieces of the 'chantransia' juvenile stage of this alga were seen in the gut contents; in March some specimens contained tightly packed pure masses of the mature thallus. A few contained myriads of *Achnanthes* and other diatoms. It is probable that *Baëtis* will eat almost any type of vegetable food.

The gut of the *Siphlonurus* nymphs usually con-

tained detritus mixed with small pieces of leaf tissue and other fragmented plant matter. In many specimens the chief food appeared to be narrow strips of *Glyceria*, and perhaps other grasses; some contained many desmids and diatoms. The favourite habitat of *Siphlonurus* is phanerogamic vegetation in gently flowing water; the masses of *Ranunculus* and *Callitriche* appear to strain out vegetable particles brought along by the current and amid their leaves desmids and diatoms multiply to form, with the accumulating debris, a kind of thick vegetable soup upon which the nymphs feed voraciously. They will also live in small pools, eating vegetable debris which accumulates on the bottom. Whether these nymphs can bite fresh vegetable material into pieces seems rather doubtful, most of the plant tissue they consume is probably fragmented by decay and the grinding action of the stones and gravel.

Ephemerella notata is the chief mayfly of the summer months and nymphs 4–5 mm. in length usually appear towards the end of May. Shallow, gently flowing water is the favourite habitat and the nymphs flourish in warm, sunny weather when the river-bed becomes covered with a thick growth of green algae and diatoms. The specimens were collected during such a period, and *Stigeoclonium*, *Closterium* and other desmids formed the greater part of their food. Of the specimens studied 82% are recorded as having fed on detritus. The amount of undigested food in the gut appeared to be much greater in specimens taken from the river early in the morning than in those collected during the afternoon, which suggests that these insects feed at night, or very early in the day.

Wissmeyer (1926), who studied the gut contents of a number of species of Ephemeroptera states that the food of *Ephemerella* includes plant tissue, *Sphagnum*, *Scenedesmus*, *Oedogonium*, *Ulothrix*, *Stigeoclonium*, diatoms and detritus. In the River Sawdde (Jones, 1949*b*, p. 153) *Ephemerella* seems to eat *Ulothrix* when a plentiful supply of this is available; the moss *Fontinalis antipyretica* is eaten when the green alga is scarce.

7. THE TRICHOPTERA

Table 4 summarizes the observations made on trichopteran larvae during the period October 1948–June 1949. *Polycentropus flavomaculatus* is the chief carnivorous type and feeds on a fair variety of insects, but the sixty specimens examined, which contained food, had accounted for only ninety-eight prey, an average of less than two per specimen. The other carnivorous trichopteran larvae found in the Rheidol include *Plectrocnemia conspersa* and *Rhyacophila dorsalis*. *Plectrocnemia* is rare, except in the uppermost reaches of the river (station A), and no specimens of this species were examined; some observations on its diet are included in the work on the River Sawdde (Jones, 1949*b*, p. 154). *Rhyacophila dorsalis* was common in the river during the spring and early summer of 1948. In May 1948, 12 specimens from station D were examined; all of these had been feeding on *Simulium* larvae and pupae which were so fragmented that it was extremely difficult to count the number eaten; a cautious estimate would be two to three larvae or pupae each. During the period October 1948–June 1949 *Rhyacophila* was very rare and only eight specimens were found. Of these five contained food, including *Leuctra*, *Hydropsyche* and *Velia*.

For the greater part of the same period *Hydropsyche* larvae were rare also, but in May 1949 large numbers of *H. instabilis* appeared in the Ponterwyd region (station B); thirty of these were examined with the result set out in Table 4. Some contained animal food but none had fed on animal food exclusively, and the majority appeared to be feeding on the abundant algal vegetation then growing on the river-bed. Generally the gut was filled with *Lemanea*, *Stigeoclonium*, *Microspora* and myriads of diatoms. The green algae were present in tangled masses, the *Lemanea* in the form of short, cleanly bitten off, cylindrical pieces. *Hydropsyche* larvae are said to trap their food with the nets they spin and also pick up food from the substratum; when algal food is abundant, as in the present instance, it would seem that the latter method is employed.

The larva of *Glossosoma boltoni* is one of the most abundant animals in the lower reaches of the main-stream. Large numbers of young larvae appeared early in May on stones in shallow, gently flowing water. These stones were thickly speckled with the small, dark patches of an encrusting blue-green alga which grows abundantly in the river and is probably the *Chamaesiphonopsis regularis* Fritsch recorded by Reese (1937, p. 405). Its cells are very small, tightly packed together, and so firmly attached to the stone that they are not removed without considerable friction. Ten of the *Glossosoma* larvae were examined and in every one the gut was found to be packed with pure masses of this alga and a little grit. On this diet the larvae seemed to grow rapidly, for by 8 June the majority had pupated. Rousseau (1921, p. 422), writing of the larvae of the Glossosomatinae says 'leur régime est typiquement carné' (régime carné = meat diet) but this appears doubtful; the scraper type mandibles of the larva and the ventral opening to its stony house seem peculiarly adapted for feeding on encrusting algae. Lloyd (1921, p. 116) states that he examined the stomach contents of a large number of specimens of *Glossosoma americanum*, and that all contained a 'light-coloured material', the cellular nature of which could not be determined.

Table 4. *The Trichoptera*

Species ...	*Polycentropus flavomaculatus* (Pict.)	*Glossosoma boltoni* Curt.	*Hydropsyche instabilis* (Curt.)	*Anabolia nervosa* (Curt.)	*Halesus radiatus* (Curt.)	*Sericostoma personatum* Kirby
Number of specimens examined	70	10	30	45	40	30
Size range (mm.)	No record	6–8	8–15	3–16	12–18	No record
Months	Oct. Apr.	May	May	Feb.–June	Feb.–Apr.	Oct.–May
Locomotion stages	A, B, D	E	B	E	E	D, E
Anterior part of the gut empty	3	—	3	—	—	4
Gut contents ignored	11	—	—	9	—	26
Gut contents						
Detritus	-	—	33	55	35	38
Leaf fragments (*Fontinalis*)	-	-	7	—	—	—
Leaf fragments (*Glyceria*)	-	-	3	73	60	
Other fragmented leaf and plant tissue	-	—	17	25	50	14
Undetermined vegetable matter	—	—	—	4	—	30
Animal						
Algae (diatoms)						
Protozoa	-	—	26	—	—	—
Nematoda	-	—	60	2	—	2
Oligochaeta	-	—	87	13	5	—
Hydracarina						2
Ostracoda						—
Gammarus				-		2
Asellus aquaticus						2
Other plant eaters	—	—	-	15	5	4
Surface animals	—	—	7	2	15	2
Larvaceans	—	—	70	2	20	—
Diatoms	—	—	80	40	40	10
Chamaesiphonopsis (?)	—	100	—	—	—	—
NEMATODA	—	—	3	—	—	—
OLIGOCHAETA	—	—	3	—	—	—
Crustacea						
Entomostraca undetermined	1	—	—	—	—	-
Gammarus not identified	—	—	3	—	—	-
Asellus	—	—	7	—	—	-
Plecoptera (nymphs)						-
Chloroperla	4	—	—	—	—	
Leuctra	13	—	—	—	—	—
Perla nymphs	—	—	—	—	—	2
Ephemeroptera (nymphs)						
Baetis	23	—	7	—	—	—
Ecdyonurus	24	—	—	—	—	—
Trichoptera (larvae)						
Hydropsyche	4	—	—	—	—	-
Larvae not identified	3	—	—	—	—	3
Sericostoma (empty cases)						
Larvae not identified	—	—	—	—		2
Coleoptera						
Dytiscid larvae	3	—	—	—	—	—
Diptera (larvae)						
Simuliidae	6	—	3	—	—	—
Tipulidae	4	—	—	—	—	—
Anthomyiidae	1	—	—	—	—	—
Ceratopogonidae	6	—	—	—	—	—
Chironomidae	1	—	—	—	—	—
Tanypodinae	1	—	—	—	—	—
Other chironomidae	14	—	13	—	—	2
Insect remains not identified	3	—	—	—	—	—
Animal food only	86	—	—	—	—	—
Animal and vegetable food	—	—	37	—	—	6
Vegetable food only	—	100	60	91	100	70
Anterior part of the gut empty or its contents digested	14	—	3	9	—	24

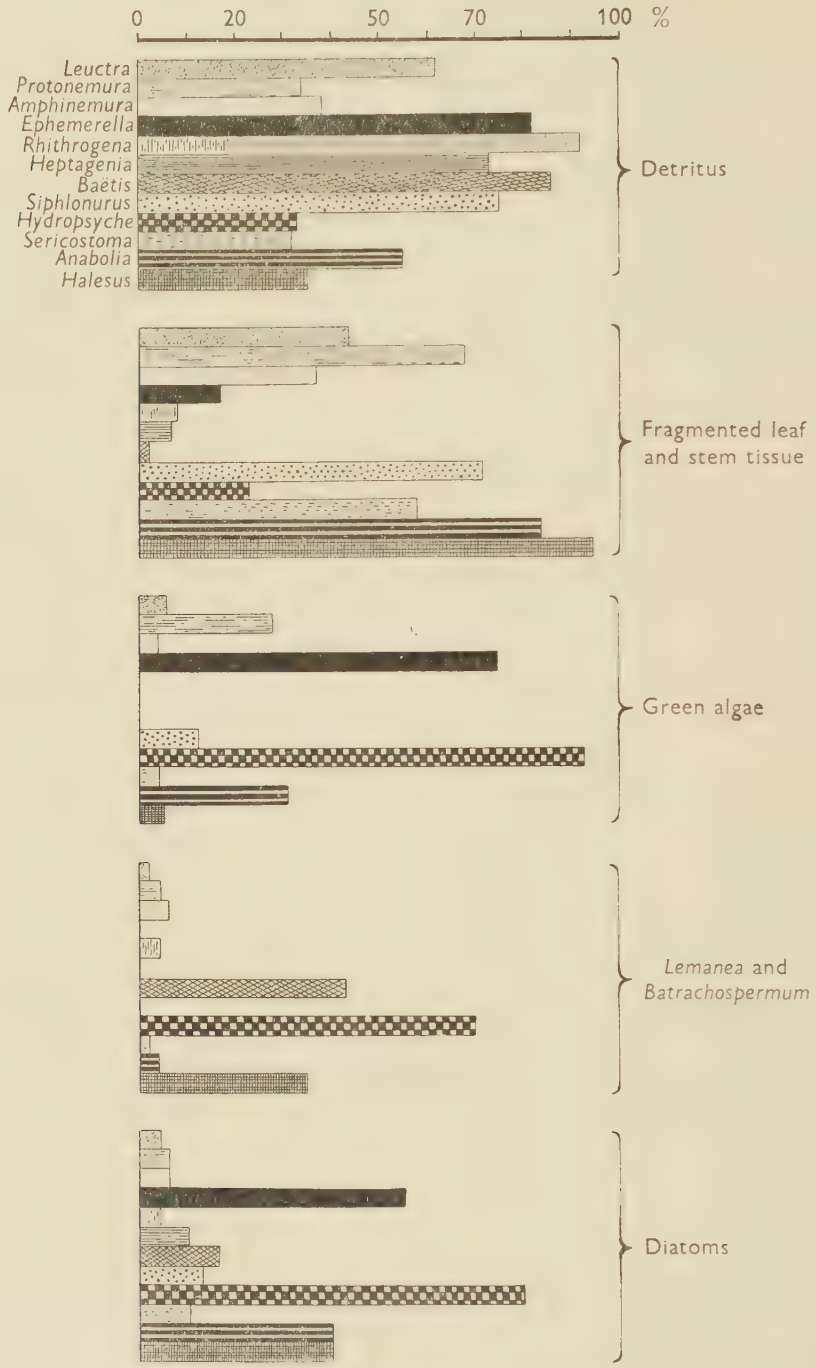


Fig. 1. The food of the phytophagous species. This includes all the species in which none of the specimens examined had fed on animal food only, with the exception of *Glossosoma boltoni*. The figures give the percentages of the specimens examined, in which food of the class indicated was found in the gut contents. 'Fragmented leaf and stem tissue' here includes dead leaves, *Glyceria*, other higher plant tissue and moss, but not the 'undetermined vegetable matter' cited in Table 4.

Anabolia nervosa is the most common limnophilid larva, and its favourite habitat in the main-stream is the *Glyceria* which grows at the margins and from which the young larvae build their cases. The gut contents, which are very bulky, are generally made up of yellow and green pieces of this grass, other fragmented leaf and stem tissue, gritty detritus and diatoms. Green algae are sometimes present, but not in significant amount. The diet of small (4 mm.) larvae examined in February and March appeared to be essentially the same as that of the large specimens taken from the river in June.

The diet of *Halesus radiatus*, which occurs during the winter in the *Glyceria* beds, is very similar; in both species the gut usually contains a fair amount of diatoms, for the most part these are epiphytes on the *Glyceria* leaves and swallowed with them or grazed off; if a leaf is taken from the habitat, its surface scraped and the scraping examined an assemblage of diatoms is discovered similar to that seen in the larva's gut.

The larva of *Sericostoma personatum* lives among stones in flowing water and among debris at the bottom of pools. Here again the gut contents are usually made up of vegetable fragments, ranging from clean cut, roughly square pieces of dead leaves to tiny parings of plant tissue one cell thick. Some specimens contained small, shapeless and opaque lumps of matter which could not be identified, but may have been scrapings from wood.

These observations are not in complete agreement with those of Slack (1936). According to Slack's table (p. 107) only four out of the eighteen *Anabolia nervosa* larvae examined had fed on leaves and 7 had eaten *Baëtis* nymphs; again in seven out of nine specimens of *Rhyacophila dorsalis* the gut contained 'mineral and organic debris'. This may have been part of the gut contents of prey eaten. There is ample evidence, of course, that trichopteran larvae may display a marked change in diet when their conditions of existence are altered; limnophilid larvae which are altogether herbivorous under natural conditions may become carnivorous or cannibalistic when confined in aquaria (Lloyd, 1921, p. 39).

8. THE COLEOPTERA

The fauna of the river includes a fair number of Coleoptera, but the larger Dytiscidae are rare except in the backwaters, and the chief species of the main-stream are the five for which gut contents data are set out in Table 5. It will be seen that *Deronectes elegans* and the three species of *Oreodytes* have a similar diet, *Baëtis* and chironomid larvae being the chief prey. *Hydroporus lepidus* collected from rock pools in the gorge section of the river, where this beetle is very common, feeds to some extent on Copepods and Cladocera.

Identification of the prey was somewhat difficult as the insects found in the beetles' crops were much fragmented and frequently the greater part of the animal eaten would be missing; in some cases only the middle part of the body of a *Baëtis* nymph would be present, the head and tail missing, and the chironomid larvae were seldom complete, some specimens containing head ends and some tail ends. Only about twenty-two of the 290 beetles examined contained pieces of more than one prey organism and cases in which a number of prey were found in the crop were very rare; one specimen of *Deronectes* had eaten four small *Baëtis* and a chironomid larva.

It would appear from the results set out in Table 5 that these small Dytiscidae feed very irregularly, for the percentage of specimens with the crop empty or with its contents digested is very high. Some specific differences are apparent; in the case of *Oreodytes davisii* only 36% of the specimens had no recognizable food in the gut and 22% had the crop full of food, while in *O. septentrionalis* 74% contained digested food or nothing and only 6% had full crops. In the case of each species the specimens were examined in batches of 5–30 on various dates. *O. septentrionalis* was one of the species studied in the work on the River Sawdde; here 22 out of 41 contained no recognizable food.

The way in which these small Dytiscidae feed is uncertain. It is stated that the Dytiscidae are voracious and insatiable carnivores which have a preference for living prey but will content themselves, on occasion, with dead animal matter. They hold captured insects with the fore- and mid-legs while the mandibles rupture their chitinous body wall and extract the soft internal tissues (Guignot, 1947, p. 24). If there is this tendency to swallow the soft parts only it would explain why the fore gut so frequently contains no recognizable matter. Many cases occurred, however, in which the prey, though fragmented, had all been eaten.

9. OTHER INSECTS

Though fairly common in the backwaters, the Odonata are somewhat rare in the main-stream of the river. The gut contents of some specimens of *Cordulegaster boltonii* (Donov.) were examined; only 11 naiads could be found, the food of which included *Halesus* larvae, *Siphlonurus*, *Baëtis*, a large dytiscid larva and one *Deronectes elegans*. The last is notable in being the only instance, in this investigation, of an adult beetle being found in the gut of another insect.

Simulium reptans (L.) was not so abundant in the spring of 1949 as in 1948 and no large numbers of

Table 5. *The Coleoptera*

Species ...	*Deronectes elegans* (Panz)	*Oreodytes davisii* (Curt.)	*Oreodytes rivalis* (Gyll.)	*Oreodytes septentrionalis* (Gyll.)	*Hydroporus lepidus* (Oliv.)
Number of specimens examined	100	50	50	70	20
Months	May	May–June	May–June	May–June	Nov.
Collection stations	E	E	B	E	C
Crop empty	55	20	36	64	35
Crop contents digested	8	16	6	10	—
Crop full and distended	8	22	12	6	No record
Gut contents:					
COPEPODA	1	—	—	—	10
CLADOCERA	—	—	—	—	5
PLECOPTERA (nymphs)					
Leuctra	—	—	2	—	—
Species not identified	1	2	4	—	15
EPHEMEROPTERA (nymphs)					
Baëtis	14	10	16	17	—
Siphlonurus (?)	2	2	—	—	—
Rhithrogena (?)	1	—	2	—	—
TRICHOPTERA (larvae)					
Hydropsyche	1	—	4	—	—
Polycentropus (?)	—	—	2	—	—
COLEOPTERA					
Dytiscid larva	—	2	—	—	—
DIPTERA (larvae)					
Dicranota	—	2	—	—	—
Dixa	—	2	—	—	5
Tanypodinae	—	—	2	—	—
Corynoneura	—	—	—	1	—
Cricotopus	—	—	4	—	—
Tanytarsus	—	—	2	—	—
Other chironomidae	17	40	18	8	30
Simulium	—	2	—	—	—
DIPTERA (pupae)					
Simulium	—	—	2	—	—
Remains not identified	4	6	4	2	15

larvae appeared until June. Twenty specimens were examined on 10 June; in every case the gut contents were very similar, consisting mainly of grit, tiny leaf fragments, *Closterium*, *Scenedesmus*, short pieces of *Stigeoclonium*, *Microspora* and other green algae, and a fair variety of diatoms. The food of *Simulium* larvae seems to depend mainly on what is available. Puri (1925, p. 298) states that larvae of different species collected from the same locality always show more or less the same type of gut contents.

10. GENERAL OBSERVATIONS

Information on the extent to which different vegetable foods are utilized is summarized in Fig. 1. During the autumn, winter and early spring of the period of observation it was evident that detritus, fragmented plant tissue, dead leaves, *Glyceria*, *Lemanea* and *Batrachospermum* were the chief foods of the common phytophagous and omnivorous insects and that the green algae and the diatoms were comparatively unimportant, though some species, *Chloroperla tripunctata* for example, would feed upon them if they were available. In 1949 the green algae and the diatoms did not appear in abundance in the river until early in May, by which time the stoneflies had bred out and *Siphlonurus* and *Ephemerella* had replaced *Rhithrogena* and *Heptagenia*. In 1948 a luxuriant growth of *Stigeoclonium* developed in the last week of February and persisted until May, but this is probably exceptional; Reese (1937), whose observations on the microflora of the Rheidol covered the period November 1933 to December 1935, found that the *Stigeoclonium* appeared in April and her quantitative data (1937, p. 395) indicate that February and March were months of sparse algal growth. Unfortunately the extent to which this very early growth of green alga in 1948 was utilized as

food by the winter Ephemeroptera and Plecoptera was not investigated, though the gut contents of some *Chloroperla* nymphs examined at this time showed that they were feeding on it.

January and February 1948 were months of heavy rainfall and it is possible that the abundance of the March growth may have been related to depletion of the benthic insects by the floods. The extent to which the plant growth of the river is limited by the feeding of the insects deserves further study. In the Rheidol, as in other rivers, the mature thallus of *Lemanea mammillosa* only develops abundantly where the current is swiftest though the alga will begin to grow on almost any part of the stream-bed where there are stones for attachment. *Lemanea* is eaten in such quantities by *Chloroperla*, *Isoperla* and *Hydropsyche* that it is possible that growth developing where the current is gentle or moderate is completely grazed down and that the plant flourishes in the most turbulent parts of the stream because here the risk of being swept away deters these insects from feeding upon it.

During the late spring and summer the green algae, particularly *Stigeoclonium*, *Microspora* and *Closterium*, become important sources of food, and some species, *Ephemerella notata* and *Hydropsyche instabilis* in particular, also feed extensively on diatoms. However, the fauna of the river does not seem to include any numerous insects in which the diatoms form the chief or only food. *Philopotamus montanus* (Donov.), which in my observation feeds mainly on diatoms, does not occur in the Rheidol, nor does *Silo nigricornis* (Pict.) which, according to Slack (1936), has a similar diet. *Silo pallipes* (Fab.) is one of the dominant insects in the Melindwr, one of the tributaries of the Rheidol (Jones, 1940, p. 194), but is very rare in the main river. The blue-green algae appear to be of no importance except in the case of *Glossosoma* already discussed; *Phormidium* was seen in the gut contents of a single specimen only (*Chloroperla*).

In the case of the Sawdde it was noted that some of the common animals of the river appeared to have some means of escaping attack by predatory species and further instances may be distinguished in the Rheidol. No Mollusca were found in any of the specimens examined; this is to be expected, for *Limnaea pereger* is extremely rare in the main-stream and the only common species, *Ancylastrum fluviatile*, is evidently protected by its shell and its ability to cling tightly to stones. The common Hemiptera of the main-stream, *Velia currens* and *Gerris najas*, live on the surface where they cannot be attacked by the predatory Plecoptera and Trichoptera. The stony case of *Glossosoma boltoni* appears to be an admirable protection against insects, though it does not prevent it being eaten by trout—Frost (1939, p. 180) in her study of the food of trout in the River Liffey found that *G. boltoni* larvae formed 9·8 % of the trichopteran larvae eaten at Straffan. The other cased trichopteran larvae of the Rheidol appear to escape attack also; this may be due partly to the protection afforded by their cases, but it is probable that their comparative immunity is mainly due to the fact that they live, for the most part, in vegetation in slowly flowing water or at the bottom of debris-laden pools, whereas the predatory Plecoptera and Trichoptera prefer the stony bed and a swift current. *Siphlonurus lacustris* is another insect which avoids these regions of danger.

In the majority of the species studied the food chain is short and uncomplicated. The general scheme for *Perlodes mortoni*, which is rather more elaborate, is shown in Fig. 2. This scheme is a little simplified by the omission, in the case of some species, of 'foods' occurring in less than 5 % of the specimens examined. It will be understood that this 'food chain' scheme applies more particularly to the Rheidol and other rivers of similar type. At the time of writing this paper a similar investigation is in progress dealing with the River Towy, a much larger river than the Rheidol and the Sawdde, with a stable bed, soft but nearly neutral water and a very rich algal and phanerogamic flora. It is hoped to present the results of this investigation in a subsequent paper together with a general discussion of the observations made on the three types of river examined in detail, but at this stage certain general conclusions may be framed. In the case of the predatory species it is evident that the polyphagous habit is general; the predatory insects feed upon the more numerous and defenceless animals; these are generally phytophagous and in swallowing its victims entire the predator obtains some supply of partially digested food, the food of the prey. This may form a considerable part of the gut contents of the carnivorous insects. The meal tends to consist of a comparatively small number of prey of large size rather than a large number of small animals, and it is possible to distinguish, at least in the Plecoptera, between species like *Perlodes mortoni* whose rapid growth appears to be associated with regular feeding so that the crop is almost always full of food, and species of slow growth (e.g. *Perla carlukiana*, whose life cycle occupies 3 years), in which feeding takes place much more irregularly, a high proportion of the specimens having the crop empty. Generally speaking, also, the predatory insects are types of high oxygen demand, living in swift, shallow water; the selection of other habitats by phytophagous species secures some degree of safety.

In the case of the phytophagous insects it is evident that detritus forms the most reliable supply of food, but it would appear that the two rivers so

far described belong to very different types as far as the origin of the detritus is concerned. In the Sawdde system where the stream-bed is occupied by great masses of bryophyte growth, much of it decaying, where flooding is infrequent and much of proportion of the detritus is of terrestrial origin. Frequent floods seem to ensure an ample supply, which accumulates among the loose stones on the river-bed; the amount available is probably a maximum in late autumn and winter, the season of

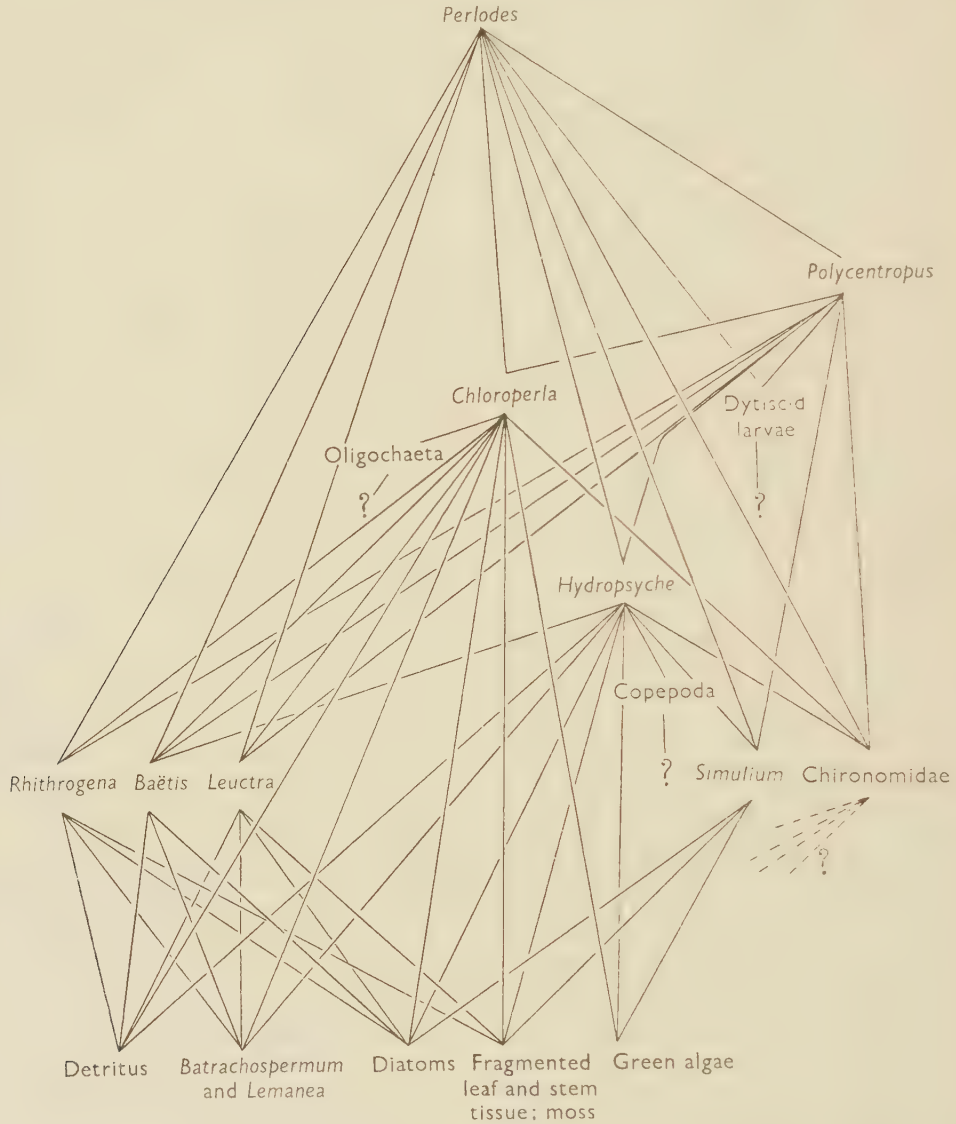


Fig. 2. The main features of the food chain of *Perlodes mortoni* and its chief prey. Based on Tables 2–5.

the water has its source in springs it is probable that the greater part of the detritus available as animal food is formed from plants growing in the water; in the Rheidol, whose shifting bed supports a much more scanty macroflora, it would appear that a high

the year when a detritus-feeding mayfly nymph peculiarly adapted for living in streams with a very swift current (*Rithrogena*) is one of the dominant animals.

Containing, as it does, a high proportion of cellu-

lose and valueless mineral matter detritus would not seem to form a nourishing diet. Insects feeding upon it have very capacious alimentary canals, feed continually and yet may display slow growth. Living algal food material is probably much more nutritious, the apparently very rapid development of *Glossosoma* larvae feeding on an almost pure diet of blue-green alga having been mentioned earlier in this paper. Some of the most successful species, *Siphlonurus lacustris* and *Baëtis rhodani*, for example, will eat detritus and almost any type of algal food, but whether a diet of living plant material results in more rapid growth has not been demonstrated. Here there would appear to be scope for observation and experiment.

2. The vegetable foods and the chief insects feeding on them are: (*a*) detritus (most phytophagous species); (*b*) dead leaves (*Protonemura meyeri*, *Amphinemura cinerea* and *Sericostoma personatum*); (*c*) *Glyceria fluitans* (*Halesus radiatus* and *Anabolia nervosa*); (*d*) fragmented leaf and stem tissue (*Leuctra hippopus* and *Siphlonurus lacustris*); (*e*) green algae (*Hydropsyche instabilis* and *Ephemerella notata*); (*f*) *Lemanea* and *Batrachospermum* (*Hydropsyche instabilis*, *Baëtis rhodani*, *Chloroperla tripunctata* and *Isoperla grammatica*); (*g*) diatoms (*Hydropsyche instabilis* and *Ephemerella notata*); and (*h*) encrusting blue-green algae (*Glossosoma boltoni*).

3. *Perlodes mortoni*, *Isoperla grammatica* and *Polycentropus flavomaculatus* are the chief predatory species; *Baetis*, *Rhithrogena*, *Leuctra* and chironomid larvae are the chief insects preyed upon. *Deronectes elegans* and the other small Dytiscidae of the mainstream feed mainly on *Baetis* and chironomid larvae. Very few animals other than insects are eaten by the predators.

Table 6. *Data on which Fig. 1 is based*

Species	Percentage of the specimens examined which contained vegetable food of the following types: Detritus	Fragmented leaf and stem tissue; moss, etc.	Green algae	*Lemanea* and *Batracho-spermum*	Diatoms
Leuctra hippopus	62	44	6	2	4
Protonemura meyeri	34	68	28	4	6
Amphinemura cinerea	38	37	4	6	6
Ephemerella notata	82	17	75	—	55
Rhithrogena semicolorata	92	8	—	4	4
Heptagenia lateralis	73	7	—	—	10
Baëtis rhodani	86	2	—	43	16
Siphlonurus lacustris	75	72	12	—	13
Hydropsyche instabilis	33	23	93	70	80
Sericostoma personatum	32	58	4	2	10
Anabolia nervosa	55	84	31	4	40
Halesus radiatus	35	95	5	35	40

11. SUMMARY

1. This paper deals with the food of the common insects in a swift, shallow, stony river with soft, acid water and is based on the examination of the gut contents of about 1300 specimens including 25 species.

REFERENCES

Butcher, R. W., Longwell, J. & Pentelow, F. T. K. (1937). 'Survey of the River Tees. Part III. The non-tidal reaches—chemical and biological.' Tech. Pap. Water Pollution Res., Dep. Sci. Industr. Res. No. 6. 189 pp. London.

Carpenter, K. E. (1924). 'A study of the fauna of rivers polluted by lead mining in the Aberystwyth district of Cardiganshire.' Ann. Appl. Biol. 11: 1–23.

Carpenter, K. E. (1925). 'On the biological factors involved in the destruction of river-fisheries by pollution due to lead-mining.' Ann. Appl. Biol. 12: 1–13.

Frison, T. H. (1929). 'Fall and winter stoneflies, or Plecoptera, of Illinois.' Bull. Ill. Lab. Nat. Hist. 18: 341–409.

Frison, T. H. (1935). 'The stoneflies, or Plecoptera, of Illinois.' Bull. Ill. Lab. Nat. Hist. 20: i–vi, 281–471.

Frost, W. E. (1939). 'River Liffey Survey. II. The food consumed by the brown trout (*Salmo trutta* Linn.) in acid and alkaline waters.' Proc. R. Irish Acad. B, 45: 139–206.

Grau, H. (1926). 'Nahrungsuntersuchungen bei Perlidenlarven.' Arch. Hydrobiol. Plankt. 16: 465–83.

Guignot, F. (1947). 'Coléoptères hydrocanthares.' Faune de France, 48. Paris.

Hustedt, F. (1930). 'Die Süsswasser-flora Mitteleuropas: Heft 10: Bacillariophyta (Diatomeae).' Zweite Auflage. Jena.

Hynes, H. B. N. (1941). 'The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs.' Trans. R. Ent. Soc. Lond. 91: 459–557.

Jones, J. R. E. (1940). 'The fauna of the River Melindwr, a lead-polluted tributary of the River Rheidol in North Cardiganshire, Wales.' J. Anim. Ecol. 9: 188–201.

Jones, J. R. E. (1949*a*). 'An ecological study of the River Rheidol, North Cardiganshire, Wales.' J. Anim. Ecol. 18: 67–88.

Jones, J. R. E. (1949*b*). 'A further ecological study of calcareous streams in the "Black Mountain" district of South Wales.' J. Anim. Ecol. 18: 142–59.

Kloet, G. S. & Hincks, W. D. (1945). 'A check list of British insects.' Stockport.

Laurie, R. D. & Jones, J. R. E. (1938). 'The faunistic recovery of a lead-polluted river in north Cardiganshire, Wales.' J. Anim. Ecol. 7: 272–89.

Lloyd, J. T. (1921). 'The biology of North American caddis fly larvae.' Bull. Lloyd Libr. 21: 1–124.

Newton, L. (1944). 'Pollution of the rivers of West Wales by lead and zinc mine effluent.' Ann. Appl. Biol. 31: 1–11.

Puri, I. M. (1925). 'On the life-history and structure of the early stages of Simuliidae (Diptera, Nematocera). Part 1.' Parasitology, 17: 295–334; Part 2, 17: 335–69.

Reese, M. J. (1937). 'The microflora of the non-calcareous streams Rheidol and Melindwr with special reference to water pollution from lead mines in Cardiganshire.' J. Ecol. 25: 385–407.

Rousseau, E. (1921). 'Les larves et nymphes aquatiques des insectes d'Europe.' Vol. 1. Brussels.

Slack, H. D. (1936). 'The food of caddis fly (Trichoptera) larvae.' J. Anim. Ecol. 5: 105–15.

Smith, G. M. (1933). 'The fresh-water algae of the United States.' New York, etc.

West, W., West, G. S. & [Carter, N.] (1904–1923). 'A monograph of the British Desmidiaceae.' 5 vols. London.

Wissmeyer, R. (1926). 'Nahrungsuntersuchungen bei Ephemeridenlarven.' Arch. Hydrobiol. Plankt. 16: 668–98.

THE DEVELOPMENT, GENERAL MORPHOLOGY AND SUBSEQUENT ELIMINATION OF BARNACLE POPULATIONS, *BALANUS CRENATUS* AND *B. BALANOIDES*, AFTER A HEAVY INITIAL SETTLEMENT

By H. BARNES and H. T. POWELL
The Marine Station, Millport

(With 3 Plates in the Text)

1. INTRODUCTION

Reference has already been made to the abundance of the larvae of *Balanus balanoides* (L.) and *B. crenatus* Brug. in the plankton, and the subsequent unusually heavy settlement on the shore and on submerged panels in the Firth of Clyde during the spring of 1949 (Barnes, 1950; Barnes & Powell, 1950). Control panels of Bakelite were exposed throughout this heavy barnacle settlement, and on such submerged panels both *B. crenatus* and *B. balanoides* settled together very abundantly, giving rise to some interesting morphological features of barnacle growth. Coincident with these observations, as part of an extensive study of colonization on cleared areas of the shore, similar morphological features were observed in *B. balanoides*.

2. *BALANUS CRENATUS* AND *B. BALANOIDES* ON SUBMERGED PANELS

The Bakelite panels (15 × 10 in.) were attached to frames and suspended 2 ft. below the surface from a raft moored close inshore near Keppel Pier. They were exposed on 25 March 1949, and the first inspection made on 15 April (21 days' exposure). The panels were thickly covered with newly metamorphosed barnacles together with some cyprids. The density of settlement was 36 per sq.cm. (mean of four counts). The next examination was made on 9 May (45 days' total exposure), when the panels were more or less uniformly covered with young barnacles. The other attached forms consisted only of mixed diatom spp. and some short filaments of *Ectocarpus sandrianus* Zanard. (also present at the previous inspection) and traces of *Cladophora* sp. and *Ulothrix flacca* (Dillw.) Thur. The panels were examined again on 10 June (11 weeks' total exposure) when the striking appearance of the densely packed barnacles suggested that a more detailed morphological examination would be of interest, and the panels were therefore withdrawn for this purpose.

The general appearance of the whole surface was a continuous crust of barnacles, the panel itself being completely obscured. As a result of differential growth outwards from the panel, the barnacle population appeared as a series of more or less uniform hummocks, the furrows between being filled with smaller barnacles, and the whole having a coralline appearance (Pl. 1, photo 1). Each hummock consisted of a dome-shaped cluster the height of which was approximately 3 cm., and the roughly polygonal base, although more variable, had a long diameter of 3·0–5·0 cm. *Balanus crenatus* appeared to have settled somewhat in advance of *B. balanoides* but, whilst the centres of the larger hummocks were occupied typically by *B. crenatus* and the surrounding furrows by *B. balanoides*, this distinction was not maintained over the whole panel.

A vertical section through one of these symmetrical hummocks (Pl. 3, photo 4) shows that they consisted of a cluster of individuals enormously elongated at the centre of the hummock, and decreasing symmetrically towards the periphery. Passing from the centre to the periphery the individuals have an increasing outward curvature. The barnacles in the furrows between the hummocks were short and cylindrical. Some 100 barnacles made up one of the larger hummocks, covering a surface area of approximately 20 sq.cm. and careful examination showed them all to be attached. It is also apparent from this photograph that a second lighter settlement of barnacles had taken place, becoming attached to the distal parts of the main settlement. The extraordinary growth in height resulting from this close-packed spat had produced barnacles the calcareous parts of which were extremely fragile, and this, together with the general feebleness of attachment, resulted in their being easily detachable. Had the exposure been continued it is difficult not to suppose that most of the individuals comprising these hummocks would have been quickly broken away by natural agencies.

3. *BALANUS BALANOIDES* ON THE SHORE

Coincident with this heavy mixed settlement on submerged panels, there was a very heavy settlement of *B. balanoides* throughout the littoral zone. Subsequently this dense settlement developed hummock formations similar to those described above, and the suggestion that few barnacles developed under these conditions would withstand prolonged exposure without breaking away from the substratum was confirmed. Bare rock surfaces became completely covered with *B. balanoides* during April and developed the characteristic hummock formations during May; breaking away of this barnacle crust began towards the end of July and by the end of November was almost complete. However, the interrelations with other forms, in particular the predatory attacks of the mollusc *Nucella lapillus* (L.) and the presence of well-developed growths of algae on the barnacles themselves, complicate the sequence of events on the shore and necessitate detailed description.

As part of a study of the colonization of artificially denuded areas of the shore, three 1 m.sq. quadrats were thoroughly cleared of their plant and animal populations during March 1949, by means of scraping followed by intensive burning with a flame-gun. The quadrats, prepared in a line down the shore between the tidal levels M.T.L. and M.L.W.N., all lay within a well-developed community of *Gigartina stellata* (Stackh.) Batt., situated on a fairly exposed, gently sloping, headland of Old Red Sandstone, just to the east of Farland Point, Isle of Cumbrae (Full National Grid Ref. 26/174541).

The clearing of the quadrats was completed by 19 March and, except for occasional diatoms, they were still quite bare when the heavy settlement of cyprids of *Balanus balanoides* occurred at the beginning of April. By 8 April the density of settlement of cyprids and newly metamorphosed barnacles was 80–100/sq.cm. over most of the surface of the quadrats, as well as on all small areas of naturally occurring relatively bare rock nearby. Attention will be particularly directed to the development of the barnacle population on the centre quadrat (*B*) situated near the tidal level E. (H.) L.W.N., although reference will also be made to the quadrats above and below it (*A* and *C*, respectively) whenever these showed important differences.

Towards the end of April and throughout May small green algae, mainly *Cladophora arcta* Kütz., developed near the outer margins of the quadrat. Small *C. arcta*, *Chaetomorpha aerea* (Dillw.) Kütz., *Ulothrix flacca*, *U. implexa* Kütz. and traces of the colonial diatoms *Navicula ramosissima* (C.Ag.) Cleve and *Fragilaria striatula* Lyngb. also occurred attached to the solid crust of barnacles, giving the whole quadrat a greenish tinge. Variable small numbers of *Nucella lapillus* (usually 6 to 12 per observation), their own shells often coated with live young barnacles, soon began to feed on the barnacles. As might be expected (Moore, 1938) quadrat *A*, at the slightly higher tidal level, carried larger numbers of *Nucella* at this time (about 50 per observation).

By 29 June (see Pl. 2, photo 2), although the general growth rate had been less than that of the barnacles on submerged panels (as was also observed by Pyefinch, 1948), the community on quadrat *B* had developed the characteristic hummock formations, which were quite independent of the contours of the underlying rock. Although all the barnacles were attached to the rock, a cluster constituting a hummock could be removed very easily, whereupon the group separated into its component individuals. The form of the barnacles and the relationship of this form to position in the hummock were essentially the same as that already described for those on the panels. On 9 June the most elongated specimens taken from near the centre of a cluster measured 11·0 mm. in height, compared with a mean height of 3·0–4·0 mm. for those at the periphery, and the diameter of the base ranged from less than 1·0 to 4·0 mm. Smaller individuals (3·0–4·0 mm. in height) attached to the distal parts of many of the longer barnacles indicated a second very much less intense settlement. Relatively small numbers of *Nucella* (6 to 12 per observation) continued to feed on these barnacles throughout June, although quadrat *A* again had very many more (up to 200 per observation). Other species developing on quadrat *B* at this time included tufts of *Enteromorpha linza* (L.) J.Ag. var. *lanceolata* Kütz. and *Cladophora arcta* around the margins and scattered in surface depressions. Young plants of these two green algae were also growing on the barnacles, together with occasional tufts of *Ulothrix flacca* and young *Porphyra umbilicalis* (L.) Kütz., traces of *Ulothrix implexa*, *Chaetomorpha aerea* and the diatom *Fragilaria striatula*.

During July and August the barnacles became rapidly overgrown with a dense growth of algae, mainly *Enteromorpha linza* var. *lanceolata* with some *E. compressa* (L.) Grev., occasional *Ulva lactuca* L. var. *latissima* DC., patches of *Cladophora arcta* and small *Porphyra umbilicalis*. The numbers of *Nucella* had increased to 50–100 per observation and occasional small *Mytilus edulis* L., *Littorina rudis* (Maton) and *L. littoralis* (L.) also occurred on the quadrat. The barnacles continued to develop beneath this algal mat, those supporting the densest growths of algae being generally smaller. A number of barnacle shells were empty, the contents presumably having been eaten by *Nucella*, but the dense growth of algae made it difficult to make a precise estimate of the extent of this predation. (On the lowest quadrat *C*, it was

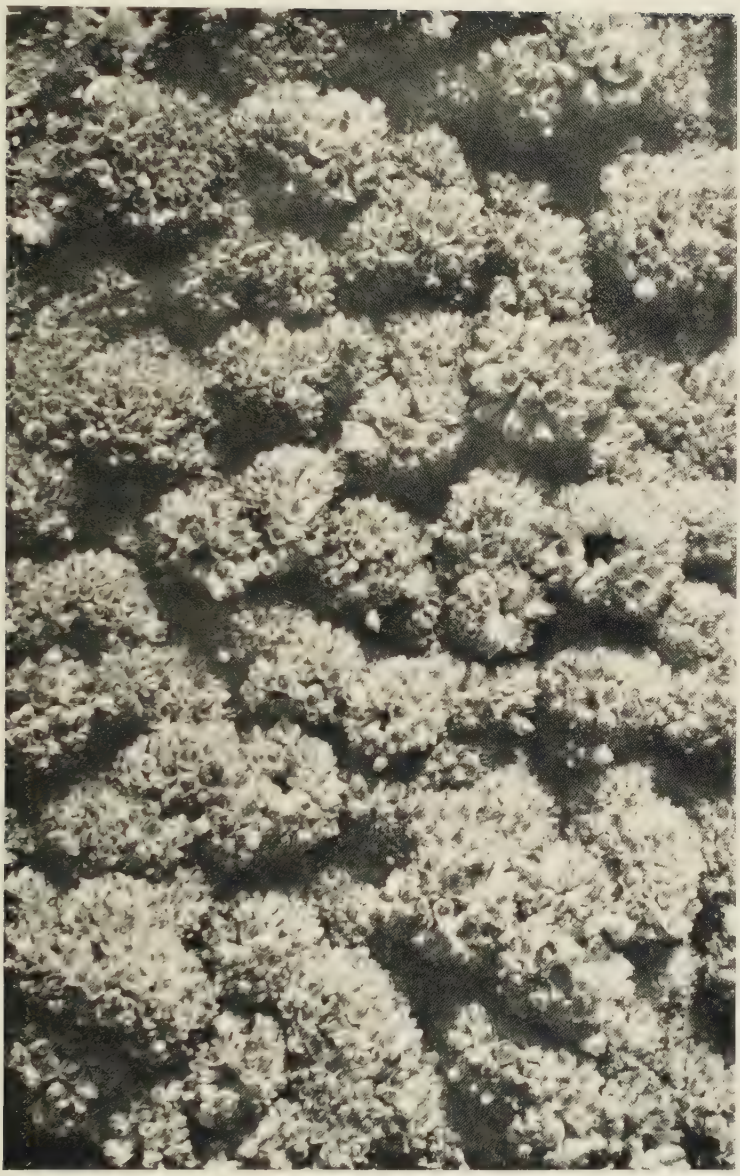


Photo 1. ×0·6. Hummock formation of barnacles (mixed *Balanus crenatus* and *B. balanoides*) growing on raft-exposed panel, after 11 weeks' exposure. *Note*: the dark furrows are actually filled with barnacles but do not show under this lighting.

Photo 2. Metre quadrat *B*: 29 June 1949. *Balanus balanoides* showing characteristic hummock formation. The dark growth in diagonal depression is *Cladophora arcta*. The lighter coloured growth in centre background and elsewhere is young *Enteromorpha linza* var. *lanceolata*, growing on the barnacles. Several *Nucella lapillus* present.

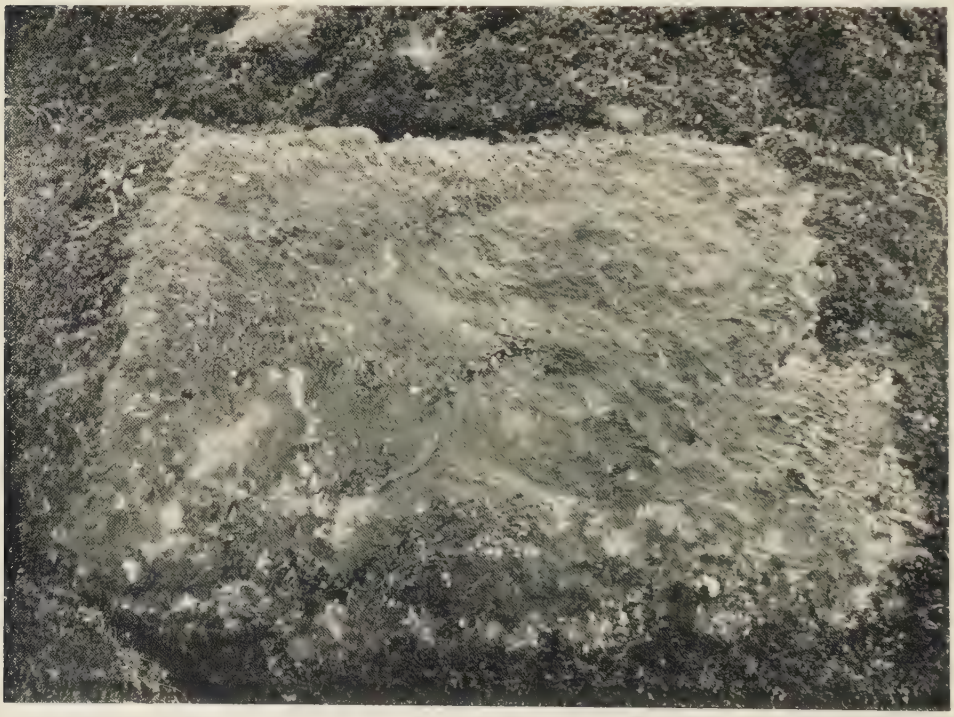


Photo 3. Metre quadrat *B*: 18 November 1949. Most of *Balanus balanoides* has been eliminated. Parts of the quadrat are very bare, while other areas are recolonized by a growth of various algae.

possible to estimate that, during August, approximately 25 % of the barnacles were dead.) Throughout this period many instances were observed of whole clusters of the most elongated barnacles becoming dislodged, leaving small areas of bare rock which soon became recolonized with young *Enteromorpha* spp., occasional *Ulothrix flacca*, and traces of *Pylaiella littoralis* (L.) Kjellm., *Fragilaria striatula* and other diatoms. The most elongated of the remaining barnacles measured 13 mm. in height, up to 5 mm. carino-rostral length (orifice) and were cylindrical or tapered more or less towards the base. They were still very thin-shelled and fragile, in contrast to the occasional more normal isolated individuals which were firmly attached to the rock.

Throughout September and October the green algae died down and were gradually washed off, together with more and more clusters of the most elongated, lightly attached barnacles, the drag of wave action on the attached fronds probably facilitating dislodgement of the barnacles. By the end of October approximately 60 % of the surface of quadrat *B* had lost its barnacle cover. The remaining barnacles were still mostly grouped in clusters of the usual form, with a maximum height of only 9·5 mm. and 5 mm. carino-rostral length (orifice). The green algae growing on these barnacles gradually included more *Enteromorpha compressa* and less *E. linza* var. *lanceolata*, both species fertile, and the numbers of *Nucella* on the quadrat dropped to an average of approximately 20 per observation throughout October. The areas of the rock surface most recently bared by the removal of barnacles quickly became recolonized with either a low green growth consisting of small *Enteromorpha compressa* and *Cladophora arcta*, or a brown filmy growth largely consisting of the diatoms *Navicula ramosissima* and *Fragilaria striatula*, with some *Ulothrix flacca* and *Pylaiella littoralis*.

It is of interest to compare the higher (*A*) and the lower (*C*) quadrats at this stage of development. Quadrat *A*, by the end of October, had lost approximately half of its barnacle and *Enteromorpha* cover, and those barnacles remaining were mostly dead, having supported large numbers of *Nucella* (100 to 150 per observation) throughout the summer. The whole sequence of colonization was very similar on this quadrat to that described for quadrat *B*, showing only minor differences in the species associated with the main colonizers. The lowest quadrat *C*, however, still carried about 85 % of its original barnacle population at the end of October. The rate of growth had always been slower at this level and the tendency towards hummock formation less pronounced. This slower rate of growth may be associated in part with the fact that this quadrat (*C*) became overgrown with algae (chiefly short, dense tufts of *Cladophora arcta*), at the time of maximum barnacle elongation throughout May and early June, whereas the upper two quadrats were not so densely covered (mainly with *Enteromorpha* spp.) until late June.

During November the sequence of events on quadrats *A* and *B* was similar. The remaining barnacles continued to be dislodged by wave action until, by the end of the month, only a few small patches of barnacles of normal form remained (4·0–8·5 mm. in height, carino-rostral length (orifice) 3·5–5·0 mm., diameter of base 8·0–11·0 mm.) and these occurred mainly near the margins. Those parts of the surface free from barnacles were comparatively bare (Pl. 2, photo 3) but were rapidly becoming recolonized with various algae. An average of 3 to 4 *Nucella* were found on quadrat *B* and up to 25 on quadrat *A*, and these were mostly confined to the marginal areas in each case.

On quadrat *C* at this time barnacles still covered about 75 % of the surface. These barnacles measured only up to 6 mm. in height, 4·1 mm. carino-rostral length (orifice), 7·0–7·5 mm. diameter of base and approximately 25 % were dead. Up to 12 *Nucella* were seen, mostly near the margins, and frequent individual and aggregated clusters of small mussels occurred with the barnacles. The algae on the quadrat included frequent tufts of large *Ilea fascia* (Müller) Fries; very frequent small buttons of *Himanthalia lorea* (L.) Lyngb.; occasional small *Cladophora arcta*, *Fucus serratus* L., *Rhodymenia palmata* (L.) Grev., *Ceramium acanthonotum* Carm., and patches of *Enteromorpha compressa*; and traces of *Cladophora sericea* (Huds.) Kütz., stunted *Scytosiphon lomentaria* (Lyngb.) Endl. and *Callithamnion roseum* (Roth) Harv. Most of the barnacles remaining on quadrat *C* were dislodged before the end of January 1950.

The suggestion drawn from the laboratory examination of the panels that these crowded colonies with their hummocks would not withstand prolonged exposure under natural conditions without becoming dislodged was thus amply confirmed for *Balanus balanoides* in the littoral zone. Attention has been directed to three experimental quadrats, but this wholesale and progressive elimination of the heavy settlement was evident throughout the whole adjacent intertidal zone.

Moore (1935) has suggested that in crowded barnacle colonies, since the barnacles are supported on all sides by their neighbours, firmness of attachment to the rock is not affected. Whilst this may be true for the strictly columnar forms as developed on quadrat *C* there is no doubt that in the extreme forms met with in hummock formation, attachment to the substratum is weak and only a small mechanical disturbance is required for their removal. Stable columnar aggregations could arise from a lighter initial settlement in which contiguity of the individuals is established after the major growth period, so that

little lateral pressure would be exerted by the bases of the compartments since they would then have ceased to expand rapidly. In intertidal zones where both the growth rate and the ultimate size is smaller than on raft-exposed panels, clearly a heavier settlement could be supported and still produce the columnar aggregations as described below. These columnar forms could also be a residue remaining from the breakdown of hummocks (see description of morphological forms below).

4. THE MECHANICS OF THE PLASTICITY OF BARNACLES

According to Darwin (1854) the growth of the shell of a barnacle such as *B. crenatus* takes place in the following way. The base is added to only around the circumference and hence increases in diameter; the compartments grow at their basal margins where they are in contact with the base and hence the shell increases in height; the compartments also grow along their lateral margins, i.e. along the edges of the radii and alae, so that the upper part of the shell also increases in diameter. (In the case of *B. balanoides* the base is membranous, but this in no way affects the argument developed; the lateral pressures set up during the early growth stages in both cases are developed by growth of the basal portions of the compartments.)

The following reconstruction would seem to explain both the hummock formation of the whole settlement and the morphological characters of the individual barnacles, developed from a heavy settlement of cyprids.

The initial settlement was heavy, and continued growth of the small normally shaped barnacles would eventually result in a contiguity of their basal parts and there would be set up considerable lateral pressure. Eventually, the result of this pressure over the whole surface of the panel would cause polygonal 'areas of pressure' to be set up. Had settlement and growth been entirely uniform, these areas would have been hexagonal and indeed in some parts of the panel the hummocks do roughly assume this pattern.

In these polygons pressure will be greatest at the centre, lateral growth being restricted, and calcareous material would be laid down only at the base of the compartments so that the barnacles grow only in height. This elongation is greatest at the centre of the polygons and leads to the formation of dome-shaped structures or hummocks.

However, as soon as the individuals in the centre of one of these hummocks, due to their greater elongation, begin to overtop their neighbours, lateral expansion of the distal parts can then take place by growth at the edges of the compartments. At the centre of the hummock where elongation has been greatest, there is thus set up a lateral pressure over the surface of the developing hummock, with the result that the surrounding barnacles become curved in their distal portions towards the outside of the hummock in a symmetrical manner (Pl. 3, photo 4). (As is clear from this photograph a second settlement had taken place (see also p. 175) and the growth of these small barnacles would contribute to the lateral pressure, tending to force apart the dome of the hummock, although it should be emphasized that the hummock photographed had more of this second settlement than was general over the whole panel. However, this is only a secondary phenomenon and does not affect the general argument above. Indeed these small barnacles growing on individuals in the centre are vertical, whilst those attached to individuals nearer the periphery lie in the same curvature as the individuals to which they are attached.)

The appearance, after further development, of any individual from such a collection will therefore depend primarily on the following factors: first, its original position with respect to its neighbours, and secondly, its ultimate position in relation to the hummocks. On this hypothesis the ultimate form of all individuals can be explained (see, for example, the forms of *B. crenatus*, Pl. 3, photo 5, which showed more clearly the whole range):

Form 1. The straight trumpet-shaped form with a moderately wide base: individuals which eventually come to lie at the centre of a hummock and not initially too crowded, so that a moderate-sized base is developed before abnormal upward growth takes place. In this material this form was entirely limited to *B. crenatus*, the slightly earlier settlement of which had allowed the development of a moderately wide base.

Form 2. As in Form 1, but with extremely narrow, almost pointed basal portion: developed at the centre of the hummock from an individual closely crowded initially and therefore never able to form a broad base before elongation.

Form 3. Curved, with moderately broad base and more or less uniformly cylindrical: those towards the periphery and sufficiently separated initially to have developed a moderately broad base before elongation.

Form 4. As in Form 3, but crowded initially and therefore with a more pointed base.

Form 5. Short and cylindrical: in the furrows between the hummocks.

Clearly a whole series of intermediate forms exists (group 6 of photo 5).

Whilst it is not possible without an examination of the original material to deny many of the subspecies that have been described (see, for example, Pilsbury, 1916), it would appear that at least in external appearance a whole series of morphologically distinct forms can be produced even within a very restricted

Photo 4. × 1·6. A median longitudinal section through a barnacle hummock showing morphological forms described on p. 178. A later settlement of *Balanus balanoides* is attached to the distal parts of the elongated earlier settlement. The calcareous bases of *B. crenatus* are seen in the foreground.

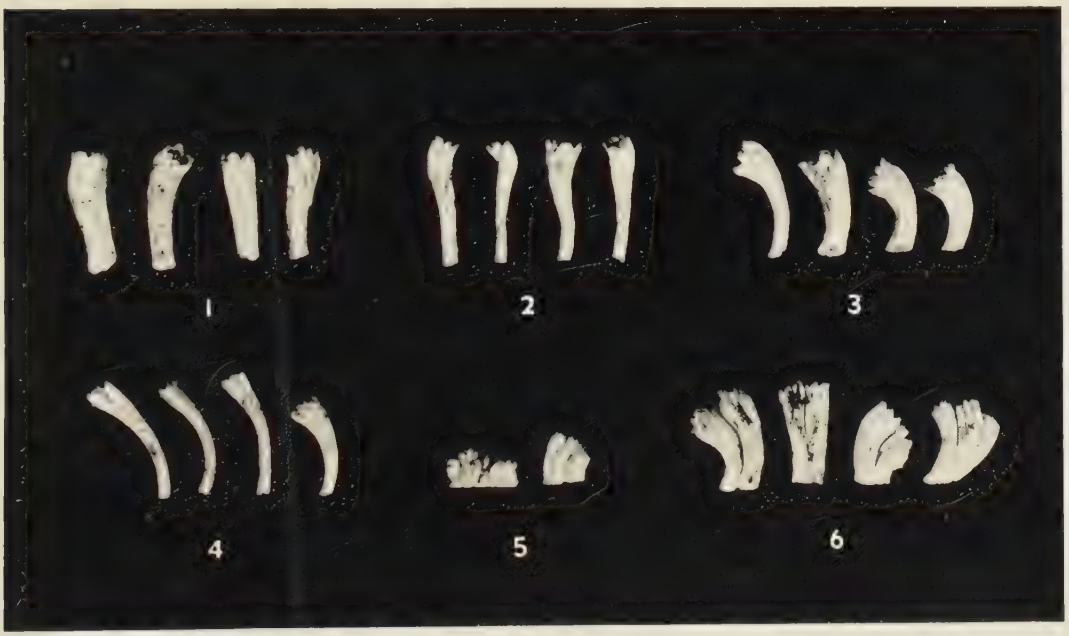


Photo 5. × 0·7. Various morphological forms of *Balanus crenatus* produced by effect of initial position and relation to subsequent development of pressure; all specimens from a single panel; see description of these forms on p. 178.

area by the interplay of mechanical forces, and it is to this that the well-known plasticity of barnacles is in no small measure to be ascribed.

Thus, Moore (1935) considers that even on external appearance *B. balanoides* var. *elongatus* Gould is a valid variety. He bases this opinion upon the fact that he found isolated specimens of an elongated form, and in particular he points out that many of his specimens were colonized around the edges by a younger brood and suggests that the bare rock spaces which existed around the elongated specimens were in some way less desirable for attachment. From our observations the presence of a second settlement of barnacles upon the elongated type (see Pl. 3, photo 4) need not indicate the presence of a bare 'unfavourable' surface around the elongated form. If the smaller and larger barnacles are from two settlements in the same year it suggests that the isolated elongated individual had been a member of a close-packed colony, thus leaving no alternative for settlement other than upon its distal parts. On the other hand, if the smaller barnacles were from a heavy settlement of a subsequent year they could have been eliminated from the rock between the more robust although elongated older individuals in the manner already described, only those attached to the upper parts of the older elongated individuals surviving. The latter phenomenon has been observed during the present study.

5. CROWDING AND CYPRID PERIODICITY

It is well known that large annual fluctuations take place both in the number of cyprids in the plankton and in the subsequent density of young barnacles on the shore (Johnstone, Scott & Chadwick, 1924; Pyefinch, 1948; Corlett, 1948). It seems probable that the wholesale elimination of the major part of a given heavy settlement and its effect in determining the numbers of available parent stock in the subsequent year is a factor which could partly account for these fluctuations, although attention to its significance has not previously been drawn.

6. ACKNOWLEDGEMENTS

We are grateful to Prof. J. E. Harris for his critical comments, and to Mr C. Davidson for assistance with the photography.

7. SUMMARY

1. A description is given of the growth of *Balanus crenatus* and *B. balanoides* on raft-exposed panels, and of *B. balanoides* on the shore, subsequent to the heavy settlement during the spring of 1949.

2. Similar morphological features are shown by both these species, but more complicating factors are present in the development of the shore population and the most important of these are discussed.

3. It is shown that extreme crowding can result in elimination of the major part of such a heavy settlement, and it is suggested that this is an influence affecting the well-known annual fluctuations in the numbers of barnacle larvae.

4. The mechanics of the production of hummocks in densely crowded barnacle populations is considered, and a series of the resulting morphological forms is described. The bearing of this upon the numerous subspecies and varieties described in the literature is discussed.

REFERENCES

Barnes, H. (1950). 'A note on the barnacle larvae of the Clyde Sea Area as sampled by the Hardy Continuous Plankton Recorder.' J. Mar. Biol. Ass. U.K. 29: 73–80.

Barnes, H. & Powell, H. T. (1950). 'Some observations on the effect of fibrous glass surfaces upon the settlement of certain sedentary marine organisms.' J. Mar. Biol. Ass. U.K. 29: 299–302.

Corlett, J. (1948). 'Rates of settlement and growth of the "pile" fauna of the Mersey estuary.' Proc. Lpool Biol. Soc. 56: 2–28.

Darwin, C. (1854). 'A monograph on the sub-class Cirripedia.' London.

Johnstone, J., Scott, A. & Chadwick, H. C. (1924). 'The marine plankton with special reference to investigations made at Port Erin, Isle of Man, during 1907–1914. . . .' London.

Moore, H. B. (1935). 'The biology of *Balanus balanoides*. IV. Relation to environmental factors.' J. Mar. Biol. Ass. U.K. 20: 279–307.

Moore, H. B. (1938). 'The biology of *Purpura lapillus*. Part III. Life history and relation to environmental factors.' J. Mar. Biol. Ass. U.K. 23: 67–74.

Pilsbury, H. A. (1916). 'The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a Monograph of the American species.' Bull. U.S. Nat. Mus. 93: 1–366.

Pyefinch, K. A. (1948). 'Notes on the biology of Cirripedes.' J. Mar. Biol. Ass. U.K. 27: 464–503.

CANADIAN ARCTIC WILD LIFE ENQUIRY, 1943–49: WITH A SUMMARY OF RESULTS SINCE 1933*

By HELEN CHITTY

Bureau of Animal Population, Department of Zoological Field Studies, University of Oxford

(With 25 Figures in the Text)

The fur trade of the Canadian Arctic is chiefly dependent upon the white or arctic fox (*Alopex lagopus*) which has a short-term fluctuation in numbers generally of three or four years. The main reason for the fox cycle is the cycle in its principal prey, the lemmings (*Lemmus* and *Dicrostonyx* spp.). The periodic disappearance of lemmings affects another of their predators, the snowy owl (*Nyctea nyctea*) which is often forced by starvation to migrate hundreds of miles to the south. In addition, sledge dogs may contract a disease with symptoms rather similar to those sometimes observed in foxes and other animals at the end of a period of abundance.

Elton (1942) describes these periodic events in northern Labrador and Ungava up to the beginning of the present enquiry in 1935–6. Reports have been published for each succeeding year up to 1942–3 and the present one brings the record up to 1948–9. In 1947 it was decided to discontinue the yearly questionnaires sent out by the Northwest Territories Administration so that 1947–8 is the last year for which there are complete data. However, information from the Annual Zoological Reports of the Hudson's Bay Company has been mapped for 1948–9. It was felt that the Canadian Arctic Wild Life Enquiry had confirmed the wide extent of, and the correlations between, cycles in lemmings, arctic foxes and snowy owls but that further advances in knowledge could come only through the work of biologists in the field.

The distribution of the various species of small rodents is discussed by Chitty & Elton (1937), Chitty & Nicholson (1942) and Elton (1942). It is to be expected that some observers fail to distinguish the species on which they report; therefore the distinction here adopted between reports on 'mice' and lemmings is not a very firm one. However this does not seriously affect the value of the information for showing changes in amount of available prey. The arctic fox is a tundra species and does not breed in the more southerly areas covered by this enquiry (groups 1 and 3) but extensive southerly migrations may take place, especially at the end of a cycle in abundance. The red fox (*Vulpes fulva*) is taken in appreciable numbers at some of the same posts as the arctic fox and is the principal species in the trade of Northern Labrador. Snowy owls breed throughout the Arctic but in many areas their numbers are evidently rather low in most years and changes in abundance are not easily appreciated.

As in previous reports the state of the various populations in each year is compared with that in the previous year, and in addition the results of all the enquiries are briefly reviewed from the beginning. The main tables on which the latest results are based are on file in Oxford and Ottawa but have not been included in this paper. Mapping of these data has been done in the usual way.

POPULATION CHANGES†

(*a*) *Lemmings and 'mice'*

1943–4. The increase in lemmings forecast by one of the observers in northern Baffin Island had materialized in 1943–4, except around River Clyde. Lemmings were also increasing and in some places were abundant in northern Quebec, although the increase was not noticed until March at Georges River. 'Mice' were reported on the increase in northern Quebec and Labrador and around the southern coast of Hudson Bay and James Bay. On the west coast of Hudson Bay lemmings were abundant in the early part of the period but were generally scarce by the spring of 1944.

Baker Lake. 'Lemming were abundant in the summer of 1943. In November they migrated, presumably toward Eskimo Point. In May 1944 they were practically non-existent. Numerous carcasses were seen lying in the glare ice on the lakes as if they had frozen to death,—none seen on land, no disease—(reports indicate they migrated towards the timber line).' (A. Lunan.)

1943–4 was the second year of reported scarcity in lemmings in Baffin Island from River Clyde south; also on Southampton Island, although a heavy migration was noted there from March through April. At

* Promoted by the Northwest Territories Administration, Ottawa. Extracts from the replies to the government enquiry are numbered; others are from post managers of the Hudson Bay Company.

† Data in Appendix 1 and Figs. 1–24.

Repulse Bay no change from the previous year's scarcity was reported but the accompanying remarks may mean that lemmings had really begun to increase during 1943–4.

Repulse Bay. 'Since the snow disappeared in June thousands of lemming have been observed at the post and reports from outlying camps at Lyons Inlet indicate lemmings are plentiful all over the country. I don't know where they came from, possibly under the snow all winter. The natives report seeing many on the sea ice a considerable distance from land and wandering in no particular direction. Those at post do not seem to have any migratory instinct just now (August 1944). There are dozens living under the buildings. They appear to be very tame or stupid as they run about our feet and forage in the grass beside the house. I have caught several with my bare hands and they made no attempt to bite. They do not enter the buildings to pilfer.' (D. Drysdale.)

Lemmings had crashed on the islands of the Western Arctic and at Bathurst Inlet so that 1942–3 had been the peak year. At Cambridge Bay no lemmings were seen during the whole year. The only report on lemmings for group 10 was of decrease around Dubawnt Lake. From Coppermine to the Mackenzie River delta (group 11) lemmings were still scarce.

1944–5. During 1944–5 lemmings had become abundant throughout northern Quebec and northern Baffin Island. 'Mice' were again reported to be plentiful in group 3 and they were said to have had an epidemic at Attawapiskat in November 1944. The two reports from northern Labrador were conflicting but at Hopedale 'mice' had been a pest. The Rev. George Harp, Moravian missionary from Hopedale, who came on furlough on 15 September 1945 said: 'In October–November 1944 mice were everywhere. My potato crop was ruined while in the ground. The mice would remove the potatoes while they were still small and make a big store of them under ground. When the spade was lifted from the ground the potatoes would fall off it like marbles. There were not many mice the previous year. There were fewer mice in the spring of 1945 but runways were still seen in the fall and mice might be numerous for a second season.'

There were also conflicting reports about lemmings from the west coast of Hudson Bay, but indications that there might be more the following season.

Chesterfield Inlet. 'Large numbers seen on the sea ice near floe edge in May.' (L. E. Corey.)

Baker Lake. 'Exceptionally scarce fall and winter, more towards spring.' (A. Lunan.)

Recovery had begun on Southampton Island while at Repulse Bay lemmings had become abundant, probably indicating that recovery had started there the previous year.

1944–5 was the first year of increase following two years of scarcity in central and southern Baffin Island where they were reported to be exceptionally abundant.

Pangnirtung. '"March of Lemming" as per radio report [to headquarters] 27 February first started around Kivitoo and Broughton Island in early February and spread southwards, reaching Cape Mercy and mouth of Cumberland Sound by April.'

The spring of 1945 brought recovery to the islands of the Western Arctic and the adjacent mainland, although the scarcity lasted through most of the season 1944–5. Lemmings were numerous at Coppermine and 'mice' were said to be abundant from Arctic Red River to the mouth of the Mackenzie River.

Coppermine. 'Very large numbers of lemming noted far out on ice where many died April 1945.'

21. *Reid Island.* 'Coppermine detachment members caught a large number to collect specimens of fleas and they nearly all had scabs all over the body and head, leaving large patches with no fur, particularly in August and September.' (E. L. Hadley.)

44. *Aklavik.* 'Very few lemming but millions of ordinary mice—in bush as well as in town. Can't take a step without seeing mice. At night all over, even in the bed.' (P. Coty.)

1945–6. Lemmings had crashed in 1945–6 in northern Baffin Island in the early part of the season, but in northern Quebec, which had been in step throughout the previous cycle, the crash was later in the year and is therefore not shown by the map. Five out of nine observers in the latter area reported increase and abundance and are mapped as such, but two of these stated that lemmings had decreased and become scarce by spring. 1944–5 had therefore been a peak year in the lemming cycle of northern Baffin Island and probably in that of northern Quebec also.

8. *Pond Inlet.* 'Sharp decrease in spring and summer 1945. Dead lemming found on the sea ice and in salt water and evidence of cannibalism.' (M. G. Owens.)

Increase was reported for the second year from central and southern Baffin Island and from Southampton Island, but at Repulse Bay lemmings had crashed at the end of the previous period.

Southampton Island. 'June 6, 1946, lemmings were seen in small numbers 5 miles north of Munn Bay the past three days, also on sea ice. There appears to be a migration from the north and it would seem that they are entering South Bay and Evans Straight, travelling over the ice. None have been seen to enter the water.' (A. W. Taylor.)

1945–6 was also the second year of recovery for the islands of the Western Arctic except at Fort Ross which was said to have few lemmings. At Bathurst Inlet increase was reported for the year as a whole, but fewer were seen in April. In the Coppermine

area there was also a second year of increase. There was little information about the rest of group 11 but 'mice' seem to have disappeared from around Aklavik.

1945–6 was the first definite year of increase since the crash in 1941–2 for the whole of the area included in group 4, i.e. west coast of Hudson Bay.

1946–7. Lemmings were very scarce throughout the Eastern Arctic during 1946–7. For northern Baffin Island and many posts in northern Quebec it was the second year of low density. However, at Port Harrison on the east coast of Hudson Bay there were signs that recovery had begun. In southern Baffin Island it was the first year of decrease, and at Pangnirtung the crash did not occur until the late winter.

Pangnirtung. 'Lemmings were abundant until December and January. Reports indicate the migration was eastward out onto Davis Strait.' (G. W. Anderson.)

At Repulse Bay where decrease had been reported in 1945 many dead lemmings were noticed in January and February 1947. They had disappeared from Southampton Island and from the region along the west coast of Hudson Bay except at Eskimo Point and Nueltin Lake where they were still abundant. 1945–6 had therefore been a peak year in southern Baffin Island, part of northern Quebec, on Southampton Island and probably in most of group 4.

'Mice' were generally scarce throughout the areas where they occur except in the interior, group 10, and in the neighbourhood of Aklavik, group 11.

It is likely that 1945–6 had been a peak year in the vicinity of Cambridge Bay, for although one of the two observers reported 'increase, abundant', he stated that lemmings were scarce during the winter months. Lemmings were still increasing in the west of Victoria Island where there was a considerable area in which the peak of the current cycle had not been passed.

1947–8. By 1947–8 the crash had occurred in the west of Victoria Island and lemmings had become scarce throughout the Western and most of the Eastern Arctic. On the northern peninsula of Quebec they had begun to increase generally and had reached abundance along the east coast of Hudson Bay. Also, at Pond Inlet they were making a rapid recovery.

1948–9. During 1948–9 the increase noted in the previous year in northern Quebec had progressed to abundance, and lemmings had also become numerous throughout northern Baffin Island. In the southern part of the island increase was reported but not general abundance. In the Western Arctic lemmings remained at a low density. 'Mice' were reported to be very numerous in Northern Labrador, northern Quebec, all around Hudson Bay and in the 'interior' of the Northwest Territories.

(*b*) *Arctic fox*

1943–4. This was a year of general scarcity in arctic foxes throughout the whole of the Eastern and Western Arctic. During 1942–3 they had crashed in northern Quebec and Labrador, around southern Hudson Bay and James Bay, at Southampton Island and in central and southern Baffin Island. 1943–4 was therefore the second year of scarcity. In 1942–3 little change in abundance was noted in northern Baffin Island and at Repulse Bay but in 1943–4 these areas had also crashed.

Arctic Bay. 'Foxes scarcer than in previous year and this was very noticeable after the end of January. Since that time fox signs have been very scarce, and the natives believe that foxes moved south late in January, although no actual migrations observed. Polar bears have been scarce this spring, although usually quite plentiful. Natives are of the opinion that the bears moved north during late March as also did the scavenger foxes who follow them.' (J. Bell.)

River Clyde. 'Fair signs of fox in Home Bay only up to January 1944. After that date scarce all over. Foxes seemed mostly around the big points, non-existent up on the land.' (J. G. Cormack.)

Foxes crashed with the lemmings on the islands of the Western Arctic and the adjacent mainland. 1942–3 had been a peak year for foxes as well as lemmings in these areas.

Along the west coast of Hudson Bay conditions varied. In 1942–3 foxes had increased between Chesterfield Inlet and Wager Bay and there were indications that recovery might be starting in this area. This did not materialize; but, at the posts along the coast south of Chesterfield Inlet, increase was noted for 1943–4.

1944–5. On the 1944–5 map the beginning of recovery in arctic fox populations was apparent, with the increase confined almost entirely to the Eastern Arctic and Subarctic. In northern Quebec all posts reported increase except Sugluk where it was not noticed until April, but foxes were still not abundant.

Sugluk. 'More foxes and better signs observed inland as far as the Povungnetuk River all winter. Towards spring, in March and April, there was a definite migration of foxes closer to the coast and burrows that have been vacant for years showed every sign of being occupied. Lemming and owl had also behaved in a similar fashion.'

In northern Baffin Island the situation was similar. Foxes were abundant only around Moffet Inlet although beginning to increase elsewhere.

For the third year in succession scarcity was reported from central and southern Baffin Island, although a slight increase was noted at Lake Harbour in October and April, and at Frobisher Bay and Pangnirtung, also in April.

Lake Harbour. 'Foxes were more abundant in October and April but almost disappeared in the interval.' (W. Ross.)

10. *Pangnirtung.* 'No foxes until around spring and exceptionally few even then. Natives claim this was the poorest year they've seen.' (J. A. W. News.)

All observers along the west coast of Hudson Bay including Repulse Bay and Southampton Island reported decrease or scarcity for the year as a whole, but at various places there had been foxes during some part of the year.

19. *Eskimo Point.* 'Foxes were fairly plentiful in fall but appeared to migrate north in November and were not replaced during the winter. There was an exceptionally large number south-east of Padlei in early fall but after migration none returned. A small influx of coloureds into this section near Padlei in March.' (E. R. Boone.)

15. *Chesterfield Inlet.* 'In early fall there were large numbers in the Rankin Inlet district. Shortly after the opening of the trapping season, November 1, they were reported to have left the district and moved elsewhere.' (L. E. Corey.)

Baker Lake. 'Foxes were fairly scarce fall and winter but almost plentiful in April and May especially in the Kazan district coming up from the south-east.' (A. Lunan.)

Repulse Bay. 'Arctic foxes were numerous during October but disappeared at end of month. One was found dead, fur very poor.' (D. Drysdale.)

The report of Mr C. L. De Lisle which covered all of Baffin Island, Somerset Island, Melville and Boothia Peninsulas agreed with the majority opinions of other observers in each of these regions but has not been included in Table 1.

1944–5 was one of the worst seasons for foxes in groups 8 and 9. From November to March very few were seen, but in April and May all posts reported increase because of migration from the north.

The position in the interior, group 10, was very obscure. Foxes were not abundant except in small patches. From Coppermine to the mouth of the Mackenzie River foxes were very scarce except just north of Coppermine and on Baillie Island. One observer in Aklavik reported an epidemic resembling 'crazy disease'.

1945–6. During 1945–6 recovery became general throughout the whole of the Arctic and Subarctic where fluctuations are known to occur. In northern Quebec increase with abundance was reported except at Wolstenholme where coloured foxes were believed to have driven out the white ones. 1945–6 was probably a peak year as by the spring there were signs of decrease at all posts from Payne Bay around the Ungava coastline to Port Harrison.

In the far northern posts of Baffin Island 1945–6 was also the second year of increase but at Pond Inlet there was a decrease after December 1945 and an epidemic similar to that in the sledge dogs was reported. 1945–6 was probably a peak year in this region as well.

Increase, reported at only three posts around southern Hudson Bay and James Bay in 1944–5, was widespread in 1945–6, but foxes were not numerous. On the coast of Northern Labrador recovery but no abundance was reported. (These areas are largely outside the normal breeding range.)

From River Clyde south on Baffin Island foxes increased rapidly during 1945–6 and the increase was expected to continue in 1946–7.

Pangnirtung. 'There has been a migration from the northwest...which is still in progress. Large numbers are in the area around the head of Cumberland Sound from Nettilling Fiord to Kingnait Fiord; also large numbers between north Pangnirtung and Padloping Fiords and south Pangnirtung and Kingnait Fiords in April and May 1946.' (G. Anderson.)

12. *Lake Harbour.* 'Signs point to an abundance next season.' (A. R. Bates.)

Increase was general in group 4, along the west coast of Hudson Bay, but foxes were not numerous except north of Chesterfield Inlet. The increase occurred in most areas in the spring months.

1945–6 was a record year for foxes in group 5. This abundance on Southampton Island and at Repulse Bay was probably linked up with that reported from north of Chesterfield Inlet and in the discussion below these two areas are considered together.

In groups 8 and 9 foxes were increasing and reaching abundance especially in the late spring. They were reported as still numerous north of Coppermine but decreasing and in poor condition. Elsewhere in group 11 they were scarce except around Cape Parry where more were seen in the spring. In the interior, group 10, few were seen, although there was a slight increase between Fort Reliance and Dubawnt Lake.

1946–7. Reports for 1946–7 confirmed that 1945–6 had been a peak year for arctic foxes in northern Quebec, as all observers in this region reported decrease and scarcity. 1945–6 had probably been the peak year for that part of northern Baffin Island around Pond Inlet, River Clyde and Igloolik, although foxes were numerous in the fall of 1946 in these regions. Around Arctic Bay and Fort Ross and on Devon Island they remained abundant during the whole year, but an epidemic among them lasting from November to March was reported from Arctic Bay. During 1946–7 foxes had disappeared from Northern Labrador and around Hudson Bay and James Bay. They had also disappeared from southern Baffin Island except in the Pangnirtung-Cumberland Sound region where they remained abundant until late

January. 1945–6, the only year of reported increase, had therefore been the peak year as well in southern Baffin Island. (Epidemic in November was noted at Cape Dorset.)

Pangnirtung. 'Lemmings and white foxes were abundant until December and January. Reports indicate the migration was eastward out onto Davis Strait. There were some indications of white fox returning from east to west in May. There was one definite report of disease in white fox in May, north of Kingnait Fiord. The animal showed no fear and attacked a native who killed it with a seal gaff.' (G. W. Anderson.)

There were many reports of disease among foxes during the late fall and winter from observers on the west coast region of Hudson Bay and at Repulse Bay and Southampton Island. It is probable that foxes were crashing throughout the whole region, but only that part north of Chesterfield Inlet reported decrease for 1946–7.

Nueltin Lake. 'Foxes migrated from east to west during November, December and January. There was an epidemic from March to May.' (C. Schweder.)

Eskimo Point. 'Disease was first noted during October in reds. During winter it prevailed generally amongst coloured and whites. A great number died affecting native fur hunts.' (E. Russell.)

Chesterfield Inlet. 'Epidemic similar to dumbrabies occurred in fall and winter. Foxes attacked other animals and humans. (L. E. Corey.)

Foxes were still increasing in the Western Arctic, groups 8–11, but epidemic disease was observed on Victoria Island from November to January.

1947–8. By 1947–8 foxes had crashed in all the regions in which they had still been abundant the previous year so that there was a general scarcity throughout the whole Arctic and Subarctic. Observers in the northern peninsula of Quebec reported that recovery had begun.

1948–9. During 1948–9 recovery became well established in northern Quebec and had begun in other regions of the Eastern Arctic except for south-eastern Baffin Island, part of which had crashed 6 months later than the rest of the group. In the Western Arctic foxes were still in the declining phase of the cycle.

(*c*) *Snowy owls*

1943–4. Snowy owls increased during 1943–4 in almost all the places showing an increase in lemmings. The increase was most apparent in Ungava, where owls became abundant in the spring, and on the west coast of Hudson Bay where they were abundant in the fall but disappeared during the winter. In northern Baffin Island owls were scarce in 1943–4, but at Moffet Inlet they were said to have become exceptionally abundant after May 1944. Throughout the Western Arctic few were seen.

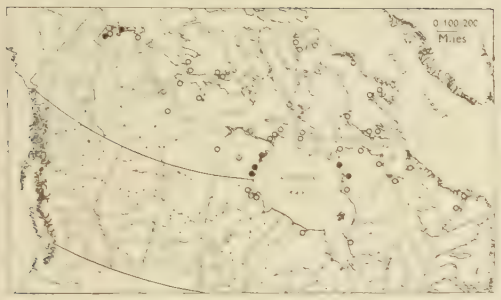
1944–5. Owls increased still further in 1944–5 and became abundant in northern Quebec; but along the west coast of Hudson Bay, on Melville Peninsula, Southampton Island and in group 3 there were very few. Recovery had begun in southern Baffin Island but was slight; farther north both increase and abundance were reported. In the western Arctic islands owls were scarce during the winter but increased in the spring when the lemmings began to recover.

1945–6. In northern Quebec snowy owls were increasingly abundant during the early part of the season, but by April four of the posts reported that they had disappeared again. Owls were scarce around southern Hudson Bay and James Bay except at Moose Factory and Albany, and vanished after December from Chesterfield Inlet. They had also declined in numbers in the north part of Baffin Island but had increased in the south although two posts reported decrease in April. In the Western Arctic they were abundant around Cambridge Bay from 1 June to 31 December after which few had been seen. From Reid Island, there was said to have been a northerly migration during October 1945. From Coppermine a southerly migration in September was reported by L. F. Semmler to have been the largest in years, 10–25 owls passing each day. These widespread reports of decrease in the Arctic coincided with the extensive southerly migration into southern and western Canada and the northern United States (Snyder, 1947) which began in mid-September 1945 and continued throughout the fall and winter.

1946–7. There was a further decline in the abundance of snowy owls during 1946–7. They disappeared from the rest of northern Quebec and from southern Baffin Island and were still scarce in northern Baffin Island. Abundance was reported from Repulse Bay, but elsewhere on the western side of Hudson Bay they had vanished. Observers on Victoria Island and the adjacent mainland reported decrease and very great scarcity but there were two reports of increase from Tuktuk and Old Crow in the far north-west. At Old Crow, on the Porcupine River, fifty owls were seen compared with three or four the previous year. The 'echo' flight of snowy owls in the autumn and winter of 1946–7 (Snyder, 1949), was larger in the west but not so concentrated in the east as it had been the previous year. This flight coincides with the crash in the Western Arctic in 1946–7 and the further decline in the Eastern Arctic.

1947–8. This was the second and, in some districts, the third year of scarcity of snowy owls. The only regions showing signs of recovery were in the northern peninsula of Quebec and in the vicinity of Pond Inlet—where lemmings had begun to recover.

Arctic fox (Figs. 1–6)



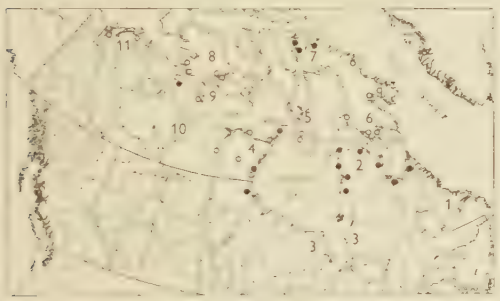
1943–4

1944–5

1945–6

Figs. 1–6. Reports about arctic fox populations in 1943–9, each year compared with the one before. Each symbol is at the approximate centre of o
large irregular spots NO CHANGE, ABUNDANT. Other black dots are Hudson's Bay Company posts. Two semicircles s

Lemming (Figs. 7–12)



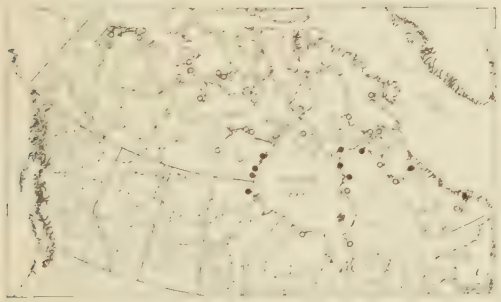
1943–4

1944–5

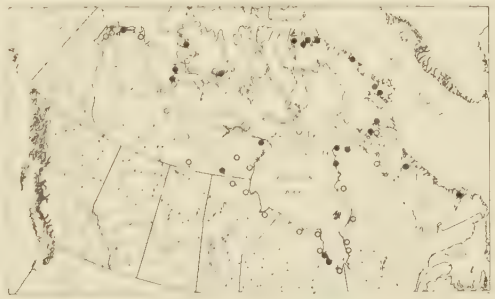
1945–6

Figs. 7–12. Reports about lemming populations in 1943–9 plotted as in Fi

Snowy owl (Figs. 13–18)



1943–4



1944–5

1945–6

Figs. 13–18. Reports about snowy ow

1948–9. By the end of 1948–9 snowy owls had become abundant in northern Quebec but had not increased further around Pond Inlet. Recovery was reported from two places in southern Baffin Island, from Southampton Island, from Nueltin Lake and two posts on southern Hudson Bay. In the Western Arctic owls were still very scarce except around Cambridge Bay and on King William Island.

(*d*) *Sledge dogs*

1943–4. A small outbreak of 'crazy disease' was reported among the sledge dogs of the Arctic in the vicinity of Aklavik, at Fort McPherson and at Liverpool Bay. The disease was said to have been caused by the bite of mad coloured foxes, which were reported to have died in large numbers around Aklavik in the spring of 1944 (and subsequently—see Cowan, 1949).

There were also several outbreaks of 'distemper' in the north-west at Liverpool Bay and in the interior around Red Rock Lake south of Coppermine. This latter outbreak was transmitted to Kugaryuak and thence to Reid Island. The disease noted at Bathurst Inlet was probably part of the same outbreak. Cambridge Bay natives reported that wolves were seen dragging their hindquarters in the spring and it was believed that they were suffering from some sort of distemper.

During 1942–3 distemper, probably from northern Alberta, had appeared in the Northwest Territories at Fort Providence and Hay River. By 1943–4 it had spread from Hay River to Fort Resolution, and from Fort Providence it went east to Fort Rae and north-west to Fort Simpson. From the latter post it spread south-west to Fort Liard and north to Fort Wrigley and then to Fort Norman which it reached in the spring. Losses were very great in some places. In Saskatchewan and Manitoba there were as usual some severe outbreaks.

1944–5. During 1944–5 there were several cases of disease amongst the dogs at Aklavik, Tuktuk, Arctic Red River, Fort McPherson and Fort Good Hope again said to have been caused by the bite of a coloured fox or a wolf. There were reports of distemper as well in these regions and farther up the Mackenzie River at Fort Norman. There was a mild outbreak of distemper in the Coppermine area and at Reid Island and Cambridge Bay on Victoria Island.

Distemper was reported in the Eastern Arctic around Cumberland Sound and Padloping on Baffin Island but there was said to have been no widespread epidemic. A more violent form of distemper was reported from Fort Selkirk in the Yukon and from Fort Rae, Fort Resolution and Rocher River on Great Slave Lake. In the northern part of the prairie provinces the outbreaks were not as devastating as in the previous year. A few cases were reported from north-western Ontario and from Quebec. At Georges River, Ungava, there was a small outbreak of a disease which caused paralysis of the lower part of the body prior to death.

1945–6. There was widespread disease among dogs in the Arctic during 1945–6. There were reports of dogs dying as a result of fox bites in the Yukon, Alaska and at Cape Parry between Tuktuk and Coppermine. A disease with symptoms like those of rabies was reported present in the Yukon, Alaska and on Victoria Island. Coloured foxes were said to have a similar disease in the Yukon, Alaska, the Mackenzie Delta and at Cape Parry. Arctic foxes were also reported 'sick' on Victoria Island and at Pond Inlet, Baffin Island.

An epidemic which may have been 'crazy' disease broke out in the vicinity of Fort Ross in January, spread to native camps in Admiralty Inlet during the latter part of February and appeared at Pond Inlet about 1 March. 30–50 % of the dogs were lost. Another outbreak at River Clyde which began in January and continued up to the end of May was said to have spread to Broughton Island in March and Padloping in April. At Nettilling Lake in April, where mortality was 60–75 %, and at Lake Harbour where it was not so heavy, a form of madness was also described.

On the Labrador coast at Cartwright and Rigolet and inland at Northwest River many hundreds of dogs died from a disease which was probably some form of distemper. The 'Periodical Accounts Relating to Moravian Missions' (June 1947) contain details of further devastations all along the Labrador coast. At Fort Chimo a number of dogs had to be shot during March and April because they were having fits.

Distemper caused losses, some severe, among the dogs in the western provinces, especially northern Alberta and around Great Slave Lake. There was also some distemper reported at Aklavik, Tuktuk and at Reid Island.

1946–7. During 1946–7 the sledge dog teams of the Arctic and Subarctic were again decimated by disease of epidemic proportions. Heavy mortality was reported from Reid Island (December to March), Coppermine east to Fort Ross (at a peak in January), the whole of Baffin Island (early winter), Southampton Island (October to April), Repulse Bay (November), and from all the posts on the north-west coast of Hudson Bay (autumn and early winter). The epidemic on Baffin Island was believed to be a continuation of that of the previous year. Arctic foxes were said to be having similar epidemics and Cowan (1949) describes abnormal behaviour among wolves.

As before, dogs seem to have shown at least two different sets of symptoms. In some cases (type 1) the head of the dog was the part most affected, with discharges from the eyes and nose, frothing at the mouth and insanity, often accompanied by viciousness and running in circles. Dogs thus affected usually died

in a very few days after the onset of the illness. Another type of illness was of longer duration (type 2). Dogs showed loss of appetite and sometimes diarrhoea, had swollen throats and became weak with paralysis of the hindquarters. At some posts dogs were described as licking the anus or vagina at the beginning of their sickness as if suffering from worms. It has been proved by Plummer (1947) that rabies was present at Baker Lake and Frobisher Bay during the 1946–7 outbreak. At Dundas Harbour, Devon Island, four out of thirty-five dogs died within two days from convulsions. It is presumed that the specimen from this post examined by Kuitunen-Ekbaum & Fleming (1949) was one of these. They found an infestation of *Trichinella spiralis*.

There were also reports of a continuation of the 1945–6 epidemic at Cartwright (south-east Labrador), and at Fort Chimo on Ungava Bay. At Povungnetuk there was an outbreak of distemper in November, and at Port Harrison a sudden localized outbreak of dog disease occurred in the spring. At Factory River, James Bay, in the summer, type 1 symptoms were noted and at Obijuan in December, type 2: both posts lost 50–60 dogs. In February at Lake River, James Bay, and York Factory, south Hudson Bay, both types were observed. At Attawapiskat, beginning in January, many dogs collapsed while in harness and at Pine River, Saskatchewan, similar cases started in February. The outbreak of distemper during the winter months in north-central Saskatchewan was very severe, causing many deaths. Elsewhere in regions where sledge dogs are used losses through disease were light, the only exceptions being Fort Providence and Fort Simpson. No disease was reported from Aklavik and the lower Mackenzie River.

1947–8. There were comparatively few reports of disease during 1947–8. At Cartwright there was a slight recurrence of the epidemic of the previous two years. At Fort Chimo rabies was reported to have occurred in June and July. At Frobisher Bay a few dogs died in December from a mild disease which caused vomiting and paralysis of the muscles of the hindlegs and rump. A few more were lost by Pangnirtung natives while hunting near the floe edge when some dogs developed a disease which made them 'crazy'.

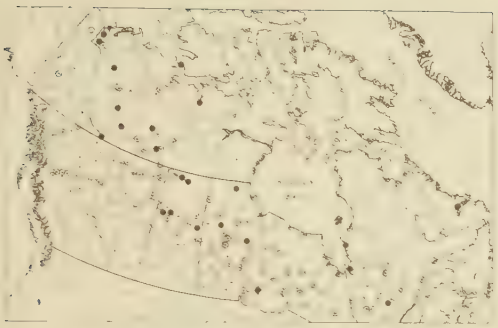
The Victoria Island outbreaks in November were said to be of acute distemper, as were those at Fort Rae and Fifth Meridian. At Moose Factory and Severn a disease which appeared to be distemper killed 30 and 65 dogs respectively. At Stony Rapids, during November to May, 80 died after an illness, which lasted only two days. In the Snowdrift area a few dogs were killed by a wasting disease lasting several months. Except for these isolated outbreaks the dog population appeared to be healthy and in some places they were breeding well and rebuilding the teams.

1948–9. A great many of the forms sent out in 1948–9 did not ask for reports on sledge dogs and among those which did there were only four reports of disease. One of these was from Arctic Bay, where an epidemic broke out in late March after certain dogs believed to be carriers had bitten other dogs in the same team. The symptoms were the same as in previous years, foaming at the mouth, viciousness and running in circles. At Padlei there was an outbreak in September of a disease which caused loss of appetite, discharging eyes and nose and 'snow-eating'. It killed 40 out of 50 dogs affected. At Seven Islands distemper began in December and wiped out 25 % of the dogs. At Fort Chipewyan the symptoms, reported as appearing first in October, were slow paralysis of the hindquarters progressing towards the head with eventual convulsions and death.

DISCUSSION

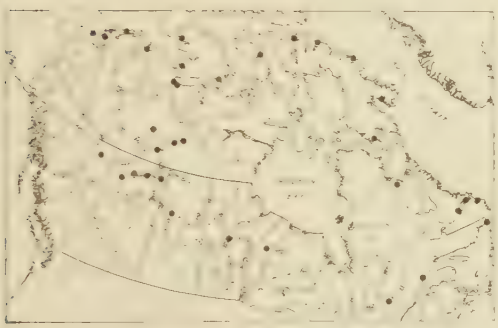
Table 1 summarizes the data on which this discussion is based, and includes figures for the thirteen years of the Enquiry, and for 1933–4, 1934–5 and 1948–9 obtained from the Hudson's Bay Company's Annual Zoological Reports. Previous reports should be consulted for details, and some further information is on file in Oxford and Ottawa.

For the purposes of this review the data have been regrouped as follows: for groups 1–3 the figures have been used without correction from each annual report. The posts of group 4 were subdivided; those north of Chesterfield Inlet were included in group 5 (Repulse Bay); the coastal posts below Chesterfield Inlet were grouped together (Eskimo Point); and the inland posts, Nueltin Lake, Padlei, Baker Lake, etc., were made into a separate subdivision (Baker Lake). Reports from Devon and Ellesmere Island have been omitted from group 7, otherwise groups 6 and 7 are as in the annual reports. The posts of the Western Arctic have been regrouped. Victoria Island (east) includes all posts on Victoria Island east of Byron Bay, those on the mainland coast from the Kent Peninsula east to Boothia Peninsula and on King William Island. Victoria Island (west) includes all other posts on Victoria Island, on adjacent islands and on the mainland coast west of Bathurst Inlet to Stapylton Bay. Under 'Interior' are grouped all replies in groups 9 and 10 referring to barren land conditions away from the coast. This regrouping is for convenience, as there is rather greater consistency among reports from these geographical divisions than from those chosen originally. Even so it is not always easy to deduce which were peak years for each species in each region. Fig. 25 and Table 1 show the rise and fall in numbers of lemming and arctic fox and



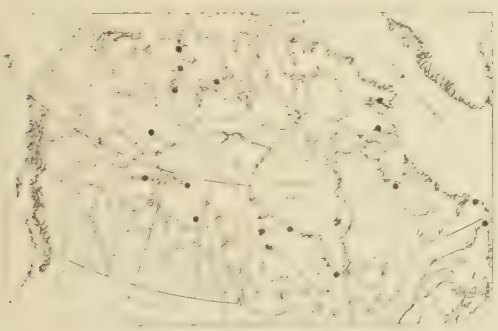
1943–4

1944–5



1945–6

1946–7



1947–8

1948–9

Figs. 19–24. Prevalence of disease among sledge dogs in 1943–9. Reports of disease, mostly serious, are shown by solid black disks; disease entirely absent by plain circles; other reports by broken circles.

the corresponding snowy owl migrations as reported by Snyder (1943, 1947, 1949) and Gross (1935, 1946, 1947).

(*a*) *The lemming cycle*

The existence of a general correlation between fluctuations in lemmings and arctic foxes has long been known (Elton, 1942) and is clearly demonstrated by Fig. 25. In some cases the two curves were simultaneous both in build up and decline of population. In others, increase in lemmings had been reported for one or two years before a corresponding increase had been noted in their predators. Similarly, a crash had occurred in the lemming population one year before a major decline in foxes took place (there was a delay of two years in northern Baffin Island on one occasion —see below). The reasons for this lag in the fox cycle have been discussed in earlier papers, especially Chitty & Chitty, 1941. It was pointed out that the difference may be real or only apparent, depending on the time of year of the lemming crash, the available alternative food for the foxes, and whether the observer's estimate is based on the actual signs and numbers seen or on the furs taken. It was partly because the present enquiry cannot clarify these matters that it was decided to terminate it. However, the enquiry has made the regularity of the lemming cycle very clear: in the areas shown in the diagram peaks mostly occurred at three- or four-year intervals.

A curve has been drawn for Northern Labrador lemmings only up to May 1941 when reports were being received from the northern posts. After that time only two or three replies came each year and were chiefly about mice in south-eastern Labrador.

(*b*) *The fox cycle*

During 1935–6, the first year of the Government enquiry, arctic foxes were scarce throughout the whole Arctic and Subarctic following a year of abundance everywhere except in Victoria Island (west) and in the western posts of Ungava which had had a crash one year earlier (Elton, 1942). Therefore 1934–5 had been a peak year for foxes generally. There was a rapid increase up to a second peak in 1937–8, only three years later, except in Northern Labrador, Victoria Island (west) and the 'Interior' where foxes remained abundant during 1938–9. After the second peak foxes were scarce in the Eastern Arctic for two seasons although increase was reported throughout the Western Arctic. The third peak occurred in 1941–2 in the Eastern Arctic except for northern Baffin Island where foxes did not crash until 1943–4, two years after the lemming crash in this area (Chitty & Chitty, 1945). The foxes of the Western Arctic also crashed in 1943–4 after three years in which almost all observers had reported increase each year. The second cycle was therefore a four-year one except in northern Baffin Island and Victoria Island (east) that there were probably five years between peaks, and in Northern Labrador only three. (The curve for the latter area may be misleading as there were no reports from the northern posts of this area after 1940–1.) The fourth peak year was 1945–6 in the Eastern Arctic but a year later, 1946–7, in the west. Thus the third cycle was a four-year one except in northern Baffin Island where there were only three years between the last two peaks.

The peak years in southern Hudson Bay and in the 'Interior' occurred at the same time as in the areas immediately to the north of them. These peaks are very sharp especially in the former area, suggesting an overflow from the north where food was becoming insufficient to meet the needs of a peak population.

Although figures for increase or abundance have been given in Table 2 for posts on the west of Hudson Bay and for Repulse Bay and Southampton Island, no curves have been drawn for these areas. There is no doubt that cycles in numbers occur locally, but it was found impossible to get a clear picture of conditions in the region as a whole.

There has been no complete series of replies from Fort Ross, and because it lies outside the other groups it is omitted from Table 2 and Fig. 25. However, it seems likely that there are regular fluctuations in numbers which coincide sometimes with those of the east and sometimes with those of the west.

(*c*) *The snowy owl cycle*

There have been reports of four major and two 'echo' flights of snowy owls from the Canadian Arctic in the period under discussion. These migrations occurred during the fall and winter months of 1934–5, 1937–8, 1941–2 and 1945–6 with 'echo' flights in 1942–3 and 1946–7. Few details have been published of the flight in 1934–5 and none of that in 1937–8 (Gross, 1935, 1947), but some information about the latter is on file in Oxford and Ottawa. Accounts of the later ones are available since the Snowy Owl Committee was formed in 1938 (Snyder, 1943, 1947, 1949; Gross, 1946, 1947).

From these publications and reports of earlier flights it is apparent that there is a major southerly migration of snowy owls at intervals of three to five years, usually every fourth year. This migration may be concentrated in the eastern part of the invasion area, scattered throughout the western part, or may involve both areas at the same time. The magnitude of the flight varies. Dymond (1947) quotes the

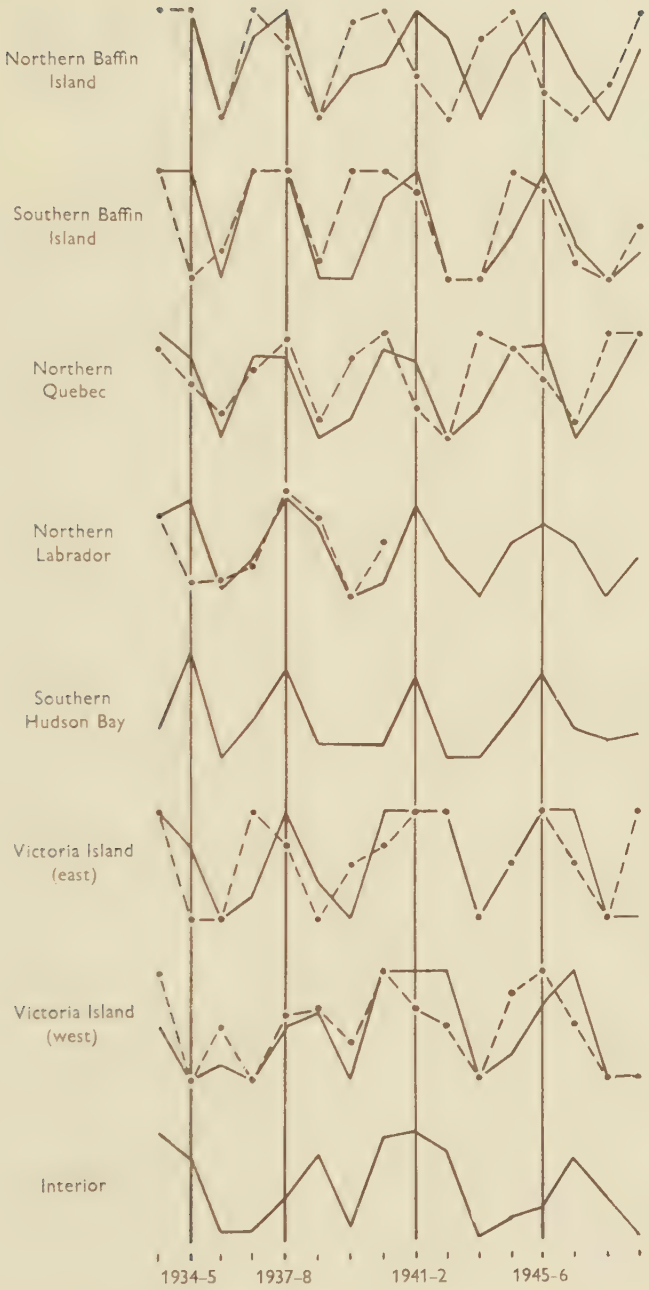


Fig. 25. Reports for 1933–49 of snowy owl migrations and of changes in numbers of lemmings and arctic foxes. Percentage of observers reporting increase or abundance is shown by broken lines (and/or dots) for lemmings, solid lines for foxes. Vertical lines are years of major migrations of snowy owls.

Table 1. *Reports of increase or abundance of lemmings* (L). *and arctic foxes* (F.). *Number of observers out of total replying*

	1933–4		1934–5		1935–6		1936–7		1937–8		1938–9		1939–40		1940–1		1941–2		1942–3		1943–4		1944–5		1945–6		1946–7		1947–8		1948–9	
	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.	L.	F.
Northern Baffin Island (group 7)*	2	2	2	2	0	0	4	3	2	4	0	0	4½	2	4	2	2	5	0	3	3	0	5	3	1	4	0	1½	1	0	3	2
	2	2	2	2	8	8	4	4	3	4	4	4	5	5	4	4	5	5	4	4	4	4	5	5	4	4	3½	3½	3	3	3	3
Southern Baffin Island (group 6)	3	3	0	1	2	0	6	6	6	6	1	0	6	0	4	3	4	5	0	0	0	0	5	2	5	6	1	2	0	0	2	1
	3	3	1	1	8	9	6	6	6	6	6	6	6	6	4	4	5	5	3	3	5	5	5	5	6	6	6	6	4	4	4	4
Northern Quebec (group 2)	9	11	4	6	2	0	8	10	12	9	2	0	8	2	6	5	2	5	0	0	8	2	6	6	5	8	1	0	7	3	4	4
	11	11	8	8	9	9	13	13	13	12	11	12	11	11	6	6	7	7	8	8	8	8	7	7	9	9	7	8	7	7	4	4
Northern Labrador (group 1)	6	6	1	9	1	1	2	4	6	11	5	7	0	0	2	1	.	5	.	1	.	0	.	1	.	2	.	1	.	0	.	1
	8	8	8	10	6	11	7	12	6	12	7	11	5	10	4	9	.	6	.	3	.	2	.	2	.	3	.	2	.	2	.	3
Southern Hudson Bay (group 3)	.	2	.	9	.	0	.	3	.	9	.	1	.	1	.	1	.	6	.	0	.	0	.	3	.	7	.	2	.	1	.	1
	.	7	.	9	.	10	.	9	.	11	.	8	.	8	.	9	.	8	.	8	.	2	.	8	.	9	.	7	.	7	.	5
Repulse Bay (group 5 and part group 4)	2	2	0	1	3	0	0	2	2	2	2	0	2	2	2	2½	1	2½	0	1	0	0	2	0	2	3	1	0	0	0	1	0
	2	2	1	1	3	3	2	2	2	2	2	2	2	2	2½	2½	2½	2½	2	3	3	3	2	2	3	3	2	2	1	1	1	1
Eskimo Point (part Group 4)	2	3	0	1	7	0	3	4	0	3	2	0	3	0	2⅔	5	0	1	1	0	2	3	2	0	3	2	1	1	0	0	0	1
	3	3	1	1	12	13	4	6	6	5½	7	6½	6	6	5	6	3½	3½	5	4	7	8	3	3	4	4	3	3	4	4	2	2
Baker Lake (part group 4)	0	1	.	.	0	0	3	1	1	4½	0	1½	0	0	3½	4½	0	0	4	1	1	0	1	0	4	4	1	2	0	0	1	1
	2	3	.	.	4	7	6	7	5	6½	6	6½	3	4	4½	4½	2	2	6	6	4	4	6	6	5	6	4	4	3	3	1	1
Victoria Island (East) (parts of groups 8 and 9)	2	2	0	2	0	0	5	1	2	3	0	1	½	0	2	3	3	3	2	2	0	0	1	1	1	1	1	2	0	0	2	0
	2	2	2	3	3	3	5	5	3	3	3	3	1	1	3	3	3	3	2	2	2	2	2	2	1	1	2	2	2	2	2	2
Victoria Island (West) (parts of groups 8 and 11)	2	1	0	0	4	1	0	0	3	2	2	3	1	0	6	5	2	3	2	4	0	0	4	1	3	2	1	2	0	0	0	0
	2	2	1	1	8	8	5	5	5	4	3	5	3	3	6	5	3	3	4	4	2	2	5	5	3	3	2	2	5	5	2	2
Interior (parts of groups 9–11)	.	3	.	3	.	1	.	1	.	3	.	10	.	1	.	11	.	3	.	8	.	0	.	1	.	2	.	5	.	1	.	0
	.	3	.	4	.	14	.	13	.	8	.	13	.	10	.	12	.	3	.	10	.	5	.	6	.	7	.	7	.	3	.	5

* See p. 186 and Fig. 7 for explanation of these groups.

following information given him by Mr L. L. Snyder:

> ...estimates of the comparative numbers involved in recent flights are as follows, the number of the 1926–7 flight being represented arbitrarily by the figure 10:

1926–7	1930–1	1934–5	1937–8	1941–2	1946–7
10	6	4	2	5	20+

The major flights may be followed by a further migration in the following year usually on a reduced scale (the so-called 'echo' flights).

These variations in the owl flights are very closely linked with the lemming cycle in the Arctic for, as Gross (1946) points out, 'the migration of owls is due to two factors; first, the great increase of the Snowy Owl population; and second, the abrupt disappearance of their chief food, the lemmings'. He states that when food is very plentiful nearly all the young owls (usually 6–8 in a nest) reach maturity; when food requires more hunting only two or three of them survive; when food is very scarce the owls may not even attempt to nest. 'In a good lemming year, practically all of the large families survive and thus the Snowy Owl population is built up to a peak along with that of the lemming' (Gross, 1947). It follows that if the lemming cycle is a short one the owl population cannot build up to such a high density. Hence, perhaps, the small size of the 1937–8 migration after a three-year cycle in lemmings in parts of the Eastern Arctic. With our present scanty knowledge it is impossible, however, to account for the great difference in magnitude between the 1941–2 and 1945–6 flights, both of which came at the end of four-year cycles. The mass migration of owls always occurs in the autumn. However, it is not known whether the lemmings crash just before the migration or some months earlier. The owls may be able to subsist during the summer on alternative food (Murie, 1929).

Replies to a questionnaire sent out by the National Parks Bureau of Canada about the 1937–8 flight suggest that the invasion was on a wide front from British Columbia to Cape Breton Island, but that it was not heavy and did not penetrate as far south as later ones. 1937–8 was a peak year for lemmings and foxes in many parts of the Eastern and part of the Western Arctic. It is possible that there was an 'echo' flight in 1938–9 that was not reported; for owls were said to have been increasing or abundant in 1938—in some parts of northern Quebec and northern Labrador, at Repulse Bay and Southampton Island and in the western half of Victoria Island—but to have disappeared by the following year. Gross (1947) states 'a certain number of owls appear each year, at least in the northern sections of the invasion area, and the individual reports of local concentrations during ordinary years tend to obscure the more pronounced cyclic invasions'.

The 1941–2 flight involved only the eastern invasion areas, the western flight being the normal yearly one (Snyder, 1947). This corresponds with reports of decrease in lemmings and owls during the winter received from northern Quebec, Repulse Bay, parts of southern Baffin Island and from northern Baffin Island. However, owls continued to increase in the Western Arctic during 1941–2 and they remained abundant in parts of southern Baffin Island, on Southampton Island and in northern Labrador where lemmings or 'mice' were still numerous. The 1942–3 'echo' flight probably reflects the disappearance of lemmings and owls from these latter regions. Although the Committee made no official enquiry Snyder (1947) says that there was a small flight in the east in the fall and winter of 1942–3. As in the previous year, invasion of the Prairie Provinces seemed to be no more than that 'which takes place practically every fall and winter'. The fact that no unusual flight was observed in the west, may mean that the peak in the Western Arctic had not been very high; or the owls may have migrated eastward (they are reported to have flown east from Cambridge Bay in November 1942).

The 1945–6 major flight was very similar to the previous one in the east although four times as large, but there was a noticeable invasion in the west as well. In the following year, 1946–7, there was a further small migration in the east and a larger one in the west. Both these migrations have been discussed earlier in this paper.

Since lemmings, 'mice' and owls had already become abundant by the spring of 1949 in some parts of the Arctic and Subarctic, a crash in the lemming populations and a mass migration of snowy owls in the winters of 1949–50 and 1950–1 could be expected. Preliminary information for 1949–50 indicates that such a flight did occur.

(*d*) *Sledge dogs*

Pandemics have ravaged arctic dog teams from time to time for at least a hundred years (Elton, 1942). The present enquiry about sledge dogs was begun to extend the evidence obtained by Elton (1931) that their diseases might be contracted from wild animals. (Braestrup (1941) quotes cases in Greenland—the last in 1919—in which disease in sledge dogs may have been contracted from arctic foxes.) Since 1935 there have been three major outbreaks of disease among sledge dogs. The first swept the northern coastline of Canada in 1938–9 and was believed to be a form of distemper spread through the travels of infected teams. There was no evidence of any relation between this outbreak and diseases in wild life.

In 1940–1 many dogs were lost along the west coast of Hudson Bay and on Victoria Island and the adjacent mainland also because of 'distemper' spread by visiting teams and again without obvious connexion with wild life. This outbreak was not on a pandemic scale.

The second and third pandemics occurred in 1945–6 and 1946–7. These have been described in this paper. In 1945–6 there were reports from many posts in the far north-west of a similar sickness among coloured foxes and wolves, and the dog disease was believed to have been started by the bite of a 'crazy' fox or wolf. The two outbreaks in the north-eastern Arctic seemed to have occurred simultaneously in widely separated regions and to have spread outwards. Arctic foxes were at a peak in both areas though no disease was noticed among them.

The major epidemic of 1946 did coincide with an outbreak of disease among white foxes of the Eastern Arctic, but on Baffin Island the dog disease was believed to be a continuation of that of the previous year. However, at the posts on the north-west of Hudson Bay where there had been no dog sickness the previous year both dogs and arctic foxes suffered from disease in the early fall of 1946.

Arctic foxes have been shown to have a peak in numbers about every fourth year, but epidemic diseases were not frequently noticed in 1933–49. The pandemics among sledge dogs have not shown a four-year periodicity and it may have been a coincidence that the outbreaks in dogs and foxes occurred together in 1946–7.

The nature of the pandemics among the sledge dogs remains to be established. Elton (1942) summarizes the facts up to 1940, since when Plummer (1947) has proved the presence of rabies in dogs at Baker Lake, Frobisher Bay and Aklavik, and in the arctic fox at Baker Lake and the wolf at Aklavik. These posts are in widely separated areas and it is suspected that rabies may be present throughout the Arctic.

Roth (1949) reported that in Greenland 70% of the sledge dogs, 30% of the polar bears and 1 bearded seal had heavy infestations of *Trichinella spiralis*. Only 3% of the arctic foxes were infected. Infection with trichinae of the polar bears of Franz Josef Land and Spitsbergen has been reported (Anon., 1948). In the Canadian Arctic this parasite was found in the polar bear and arctic fox (Parnell, 1934) and more recently in the polar bears of Southampton Island (Brown *et al.* 1949) and in sledge dogs at Sugluk in northern Quebec and at Dundas Harbour, Devon Island (Kuitunen-Ekbaum & Fleming, 1949). Connell (1949) points out that trichinosis is now recognized as a major health problem in the Arctic.

Gould (1945) reviews the literature and quotes symptoms observed in an infected dog. These were bloody diarrhoea, occurring 2 weeks after infection, together with restlessness, swelling of the eyes, ruffling of the fur, inability to walk after several days, cramps, purulent secretion from the inner canthi, drooling at the mouth, and tonic and clonic convulsions of the neck muscles. Many of these symptoms have been described during some of the outbreaks of dog sickness in the Arctic, and in view of the high rate of incidence of *Trichinella* infection it would not be surprising if this parasite proved to be an important component of disease in sledge dogs.

So far there is no proof that the epizootic fox encephalitis discovered by Green, Ziegler, Green & Dewey (1930) exists among the wild foxes of the north. Inoculation with the virus of this disease produces an infection in experimental dogs, the symptoms of which have been described by Green & Shillinger (1934). Chaddock (1947) has succeeded in isolating the virus of this infection from carcasses of dogs from different places in the U.S.A. These dogs had died from a distemper-like infection which had not responded to the usual anti-distemper treatment. The symptoms of fox encephalitis resemble those reported from time to time as exhibited by sledge dogs and 'crazy' foxes, but the animals at the posts where rabies was recently identified were also said to have been 'crazy'. It is difficult even for a trained veterinarian to distinguish between fox encephalitis and the central nervous system type of distemper—and from the descriptions given in the reports it is altogether impossible.

'Distemper' is rampant among the dogs of the bush posts and has been transmitted to the north by visiting teams of infected dogs. All the various types of symptoms of dog disease have been described both from bush posts and from the arctic. It may be that the virus of epizootic fox encephalitis is one of the causes of epidemics, but only detailed laboratory tests could prove it. However, there has been no four-year periodicity in pandemics in the north corresponding to peaks in arctic fox numbers. On the other hand, there have been outbreaks in the south with identical symptoms and proof of transmission of disease from south to north. A connexion between the sledge dog pandemics and the arctic fox-lemming cycle is therefore unproven.

ACKNOWLEDGEMENTS

We are very grateful to those who have given us our information for so many years and to those who have organized its collection. In particular, we wish to thank Mr R. A. Gibson, Deputy Commissioner of the Northwest Territories, Ottawa, Mr R. H. G. Bonnycastle and Dr L. Butler of the Hudson's Bay Company, Winnipeg. Our thanks are also due to the Governor and Committee of the Hudson's Bay Company who have made the Bureau a grant in aid of this research.

ing snowy owl populations in 1943–9.

ith ear immediately preceding. (Each year ends 31 May.)

ern ic

5			6						7						Total							
46 7	47–48	48–49	43–44	44–45	45–46	46–47	47–48	48–49	43–44	44–45	45–46	46–47	47–48	48–49	43–44	44–45	45–46	46–47	47–48	48–49	43–44	44–4
A																						
.	.	.	2	6	1	.	1	.	3	3	1	.	2	5	15	35	8	4	11	14	39
1	.	5	3	.	4	4	3	4	1	.	2	3	1	27	18	5	23	23	8	75	47
.	1	.	.	.	1	.	.	.	1	1	1½	.	.	4	5	4	5½	4	3	11	13
1	1	5	5	6	6	4	4	4	5	4	4½	3	3	36	38	44	36½	31	22	100	100
L																						
.	1	.	5	5	.	.	2	3	5	1	.	1	3	14	21	20	3	8	11	45	73
.	.	5	.	1	5	4	1	1	.	3	3	2	.	11	3	9	19	10	1	35·5	10
1	.	.	.	.	1	.	1	.	.	.	1½	.	.	6	5	3	5½	5	5	19·5	17
1	1	5	5	6	6	4	4	4	5	4	4½	3	3	31	29	32	27½	23	17	100	100
Sn																						
.	1	.	4	5	.	.	2	.	5	.	.	1	.	10	18	18	1	7	12	29	49
.	.	4	.	1	6	4	1	.	.	3	1	1	2	12	9	13	23	13	5	35·5	24
1	.	1	1	.	.	.	1	4	.	1	3	1	1	12	10	13	11	11	6	35·5	27
1	1	5	5	6	6	4	4	4	5	4	4	3	3	34	37	44	35	31	23	100	100

stern

	11					Total						Percentage					
48–49	44–45	45–46	46–47	47–48	48–49	43–44	44–45	45–46	46–47	47–48	48–49	43–44	44–45	45–46	46–47	47–48	48–49
.	1	1	4	.	.	3	3	7	10	1	.	21·5	17·5	47	74	9	.
1	5	3	.	3	2	9	11	4	1	10	9	64·5	65	26·5	7	91	82
2	.	1	.	.	.	2	3	4	2½	.	2	14	17·5	26·5	19	.	18
3	6	5	4	3	2	14	17	15	13½	11	11	100	100	100	100	100	100
.	3	2	.	.	.	.	8	7	4½	2	2	.	44·5	63·5	43	20	22
.	1	.	.	.	1	7	3	1	1	5	5	63·5	16·5	9	9·5	50	56
2	3	1	3	3	.	4	7	3	5	3	2	36·5	39	27·5	47·5	30	22
2	7	3	3	3	1	11	18	11	10½	10	9	100	100	100	100	100	100
.	3	3	1	1	.	.	5	6	1	1	2	.	29	40	9	11	22
.	1	.	.	2	.	8	2	1	2	6	4	61·5	12	6·5	18	67	45
2	3	3	2	.	1	5	10	8	8	2	3	38·5	59	53·5	73	22	33
2	7	6	3	3	1	13	17	15	11	9	9	100	100	100	100	100	100

SUMMARY

1. This paper concludes the Canadian Arctic Wild Life Enquiry which has been based on questionnaires sent out annually by the Northwest Territories Administration, Ottawa, and by the Hudson's Bay Company, Winnipeg.

2. Arctic foxes were mostly at a peak in 1933–4. Since then there have been three further peaks. These occurred in 1937–8, 1941–2 and 1945–6 in northern Quebec and other areas. Some regions were out of phase with the rest, but synchronous fluctuations occurred over vast areas of the Eastern and Western Arctic.

3. Lemming peaks were reported for the same year as those of the fox or one year earlier.

4. Snowy owl migrations coincided with the disappearance of the lemming populations of the Arctic.

5. Sledge dogs suffered three pandemics. There was no obvious connexion with the periodic decrease of lemmings and arctic foxes.

REFERENCES

(*a*) *Chronological sequence of previous reports (in* J. Anim. Ecol.)

Chitty, D. & Elton, C. (1937). 'Canadian Arctic Wild Life Enquiry, 1935–36.' 6: 368–85.

Chitty, D. (1938). 'Canadian Arctic Wild Life Enquiry, 1936–37.' 7: 381–94.

Chitty, D. (1939). 'Canadian Arctic Wild Life Enquiry, 1937–38.' 8: 247–60.

Chitty, D. (1940). 'Canadian Arctic Wild Life Enquiry, 1938–39.' 9: 227–42.

Chitty, D. & Chitty, H. (1941). 'Canadian Arctic Wild Life Enquiry, 1939–40.' 10: 184–203.

Chitty, D. & Nicholson, M. (1942). 'Canadian Arctic Wild Life Enquiry, 1940–41.' 11: 270–87.

Chitty, H. (1943). 'Canadian Arctic Wild Life Enquiry, 1941–42.' 12: 163–72.

Chitty, H. & Chitty, D. (1945). 'Canadian Arctic Wild Life Enquiry, 1942–43.' 14: 37–45.

(*b*) *Other references*

Anon. (1948). 'Trichinosis from polar bear meat. Arctic, 1: 144.

Braestrup, F. W. (1941). 'A study on the arctic fox in Greenland: immigrations, fluctuations in numbers based mainly on trading statistics.' Medd. Grønland, 131, No. 4: 1–101.

Brown, M., Cronk, B., de Sinner, F., Green, J. E., Gibbons, J. E. & Kuitunen-Ekbaum, E. (1949). 'A note on trichinosis in animals of the Canadian Northwest Territories.' Canad. Publ. Hlth J. 40: 20–1.

Chaddock, T. T. (1947). 'Encephalitis in the fox and in the dog.' Vet. Med. 42: 475–8.

Connell, F. H. (1949). 'Trichinosis in the Arctic: a review.' Arctic, 2: 98–107.

Cowan, I. McT. (1949). 'Rabies as a possible population control of Arctic Canidae.' J. Mammal. 30: 396–8.

Dymond, J. R. (1947). 'Fluctuations in animal populations with special reference to those of Canada.' Trans. Roy. Soc. Can. 41: 1–34.

Ekbaum, E. Kuitunen- & Fleming, Z. W. (1949). 'A note on trichinosis in dogs of the Canadian north.' Canad. Publ. Hlth J. 40: 514–15.

Elton, C. (1931). 'Epidemics among sledge dogs in the Canadian Arctic and their relation to disease in the arctic fox.' Canad. J. Res. 5: 673–92.

Elton, C. (1942). 'Voles, mice and lemmings: problems in population dynamics.' Oxford.

Gould, S. E. (1945). 'Trichinosis.' Springfield, Ill.

Green, R. G. & Shillinger, J. E. (1934). 'Epizootic fox encephalitis. VI. A description of the experimental infection in dogs.' Amer. J. Hyg. 19: 362–91.

Green, R. G., Ziegler, N. R., Green, B. B. & Dewey, E. T. (1930). 'Epizootic fox encephalitis. I. General description.' Amer. J. Hyg. 12: 109–29.

Gross, A. O. (1935). 'The snowy owl migration, 1934–35.' Auk, 52: 310.

Gross, A. O. (1946). 'Snowy owl invasions.' Bull. Mass. Audubon Soc. 30: 29–32.

Gross, A. O. (1947). 'Cyclic invasions of the snowy owl and the migration of 1945–46.' Auk, 64: 584–601.

Murie, O. J. (1929). 'Nesting of the snowy owl.' Condor, 31: 3–12.

Parnell, I. W. (1934). 'Animal parasites of north-east Canada.' Canad. Field-Nat. 48: 111–15.

Plummer, P. J. G. (1947). 'Preliminary note on arctic dog disease and its relationship to rabies.' Canad. J. Comp. Med. 11: 154–60.

Plummer, P. J. G. (1947). 'Further note on arctic dog disease and its relationship to rabies.' Canad. J. Comp. Med. 11: 330–34.

Roth, H. (1949). 'Trichinosis in arctic animals.' Nature, Lond., 163: 805–6.

Snyder, L. L. (1943). 'The snowy owl migration of 1941–42: a report of the Snowy Owl Committee.' Wilson Bull. 55: 8–10.

Snyder, L. L. (1947). 'The snowy owl migration of 1945–6: second report of the Snowy Owl Committee.' Wilson Bull. 59: 74–8.

Snyder, L. L. (1949). 'The snowy owl migration of 1946–7: third report of the Snowy Owl Committee.' Wilson Bull. 61: 99–102.

REVIEW

A SCANDINAVIAN JOURNAL FOR ECOLOGY

Oikos: Acta Ecologica Scandinavica. Vol. 1, Fasc. 1 and 2, 1949. 293 pp. Chief Editor: **Dr Erik Dahl**; Managing Editor: **Dr Helge O. Backlund**; both of the Zoological Institution of the University, Lund, Sweden. Publisher: Ejnar Munksgaard, Copenhagen, Denmark. Price 40 Danish crowns annually.

British ecologists, at any rate those mainly studying animals, must for some time have realized vaguely that they were losing much by their inability to follow the research results from countries round the Baltic. The tendency recently to publish some of the more important monographs from this area in the English language has only made us more eager to obtain a fuller picture of the ideas and methods that are being developed there. The new journal reviewed here is a first-class enterprise which should be noted and encouraged by ecologists, not only because of the obviously good quality of the research put in it, but also for the most valuable reviews of Scandinavian work much of which is wholly or partly inaccessible to us, through source or language. Of the eighteen original papers contained in this first volume, fourteen are in English and four in German. The Editors are in the glorious and, I am afraid, ephemeral stage of publishing short and readable papers, and the authors are asked to limit themselves to 32 pages of print, except for any special supplements that may be appended. The average length of the papers printed is about 13 pages. Besides the two Editors mentioned by name above, there is an editorial board with ecologists from Denmark, Norway, Iceland, Sweden and Finland.

The range of subjects includes measurement of the environment itself, some plant ecology, but mainly animal ecology. The emphasis, as would be expected from the trends of European ideas, is rather on distribution and the direct physical relationships of organisms to their habitats, than on the dynamic aspects of population change and control. This is probably a good thing at the moment, since British work has tended to ignore the quantitative measurement of the animal environment, though expanding further into population analysis.

Four papers deal with soil ecology: J. Iversen (Denmark) puts forward some points about root ecology; O. Vaartaja (Finland) gives a thorough study of the temperature conditions at the surface of heathland soil (on which the heat may reach 50 or 60° C.), and brings out some important points about the conductivity errors in interpreting thermocouple results; O. Renkonen (Finland) describes a method of sorting soil and litter nematodes in water which is claimed to produce 90–95 % of the worms from samples; E. Rennenfelt (Sweden) has studied the inhibiting effects of soil fungi and bacteria upon *Polyporus annulosus*, the root-rot fungus of spruce.

As we might expect and hope, a group of papers deals with animals in fresh water and within the Baltic system. P. Bondesen and E. W. Kaiser describe the present occurrence of *Hydrobia jenkinsi* in Denmark, where it appears to have still a rather restricted distribution in brackish and fresh waters. K. Thomasson has discovered several micro-organisms in the fresh water Lake Mälaren in Sweden which appear to be relicts from brackish water. These include a ciliate, two rotifers and some diatoms. S. G. Segerstråle deals with the brackish-water communities of Finland, and illustrates them with 'Petersen' photographs of the different community organisms. B. Bérziņš comments on the influence of swings in temperature upon the movements of some Baltic animals in the Riga seas.

Two very interesting papers are concerned with the influence of agricultural conditions upon organisms. T. Gislén has traced the decline in abundance and range of *Melampyrum arvense* on the mainland of Sweden, and its relation to the changing plant communities (which include its possible hosts), the occurrence of a seed-consuming agromyzid fly, and other factors. O. Hammer contributes a very valuable study of the relation of hive-bees to red clover in Denmark. It may surprise some British ecologists to know that the red clover, if it is a variety with short enough corolla, can be a honey source of dominant importance to the hive-bee. This research includes also a great deal of information about the conditions of nectar flow and the behaviour of the bees.

The other papers are by G. Svärdson on competition among birds as indicated by the distribution of species pairs in Scandinavia; by B. Petersen and J. E. Treherne on colour forms of the grasshopper *Omocestus viridulus* and their ecology in Sweden; by P. Palmgren (Finland) on cycles in numbers of small mammals and birds; by O. Renkonen (Finland) on some of the general concepts of measuring community association among insects; by G. Herrström on the light referendum of the carabid beetle *Agonum dorsale*; by U. Perrtula on the distribution and ecology in Finland of certain species of plants with markedly eastern distributions (two parts); and an excellent study by E. Bro Larsen of the effects of a group of cold winters upon the vegetation (especially *Agrostis alba*) and soil animals of a maritime complex.

The journal is printed and produced in first-class form, is well illustrated by diagrams and gives a number of full tables of data. The photographs are less satisfactory, as they are printed on the same paper as the text. One or two coloured photographs have been included, and seem useful for their particular purposes, though not exactly realistic in shades. These are small criticisms. As a whole, the journal will take its place as part of the normal reading of ecologists, and its future should be well assured.

C. ELTON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Several papers omitted in the last few years are being noticed in this and following issues. Papers in the *Journal of Animal Ecology* itself are not dealt with. Readers can aid the work greatly by pointing out omissions and sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, Department of Zoological Field Studies, 91 Banbury Road, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by R. Bainbridge, H. F. Barnes, P. G. Corbin, G. I. Crawford, A. E. Ellis, C. Elton, I. M. Goodbody, Miss U. M. Grigg, A. Macfadyen, C. Matheson, E. Nelmes, E. R. Parrinder, H. G. Vevers and Miss G. Watt; checking by B. M. Hobby; abstracting and editing by R. S. R. Fitter.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

	PAGE
1. Ecological surveys and the relations of animals to habitat conditions	196
(*a*) Marine and brackish	196
(*b*) Fresh water	197
(*c*) Land	198
(*d*) Small islands	200
2. General reports and taxonomic studies of use to ecologists	200
3. Parasites	201
4. Food and food habits	202
5. Population studies	202
6. Migration, dispersal and introductions	202
7. Reports of organizations	204

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Ainsworth, G. H. & Lord, J. (1940). 'Some bird notes from the coast in winter.' Naturalist: 135–6.

A brief account of the effect of the abnormally severe winter on sea birds near Bridlington.

Kitching, J. A. (1950). 'Distribution of the littoral barnacle *Chthalamus stellatus* around the British Isles.' Nature, Lond. 165: 820.

This species, which is at the northern edge of its range in the British Isles, occurs on the south coast from Dorset westwards, up along the west coast of Great Britain and round to Caithness. An earlier hypothesis

attempted to link this with the influence of Atlantic water. It is now suggested that the range is limited by winter temperatures of the water and also of the air (to which the species is also exposed). The best fit is to the February surface-water isotherm of 7° C. and the February mean daily minimum air temperature of 3·3° C. Disagreements with these limits on the west coast of Scotland are provisionally attributed to inadequate meteorological data.

McMillan, (Mrs) N. F. (1950). 'The resistance of *Littorina saxatilis* (Olivi) to lowered salinity.' J. Conchol. 23: 107.

Experiment to test the effect of progressively decreased salinity on a species of winkle.

Mason, A. G. (1949). 'Census of guillemots on Gt. Saltee Island.' Irish Nat. J. 9: 336–7.

Population of guillemots (*Uria aalge*) is estimated to be between 23,000 and 28,000. The total bird population of the island is estimated to be not more than 47,000 individuals. The puffin (*Fratercula artica*) has increased since 1943, but it is still not as numerous as in 1931.

Nicholas, W. W. (1940). 'Birds of Bempton cliffs. A brief survey extending from Flamborough Head to Bempton End, May 31st, June 1st and 2nd, 1940.' Naturalist: 217–19.

The status of the breeding birds in 1940 and a comparison with conditions twenty-five years ago.

Procter, C. F. & Mason, C. W. (1940). 'Sea-birds and the oil problem.' Naturalist: 33–4.

Factors which lead to the oil polution of sea-birds' feeding grounds off the Yorkshire coast with consequent high mortality especially among guillemots, razorbills and kittiwakes.

Rees, C. B. (1949). 'Continuous plankton records: The distribution of *Calanus finmarchicus* (Gunn.) and its two forms in the North Sea, 1938–39.' Hull Bull. Mar. Ecol. 2 (14): 215–75.

An account is given of the means of distinguishing two forms of *Calanus finmarchicus*, named 'finmarchicus' and 'helgolandicus' after their correspondence with the species *C. finmarchicus* (Gunn.) and *C. helgolandicus* (Claus). The distribution of the forms at a depth of 10 m. in the North Sea during 1938–9, as recorded with the Hardy Plankton Recorder, is analysed and their life histories and size variations are dealt with. It is suggested that their distributions may be accounted for by temperature differences in the water, and that the two forms constitute a cline. An appendix summarizes data on the distribution of *Calanus* in the southern North Sea during 1932–9.

Southward, A. J. (1950). 'Occurrence of *Chthalamus stellatus* in the Isle of Man.' Nature, Lond. 165: 408–9.

This high-water barnacle found to be generally distributed round the Isle. It may have fluctuated in its occurrence there. A map shows a certain amount of agreement between the eastern limit of the barnacle in the British Isles and the February isotherms of mean air temperatures between 40° and 42° F.

Thompson, J. L. Cloudsley- (1948). '*Hydroschendyla submarina* (Grube) in Yorkshire: with an historical review of the marine Myriapoda.' Naturalist: 149–52.

Four specimens of *H. submarina* were collected at Cloughton Wyke in August 1947. This very rare species has not been found in the British Isles since 1889 when it was discovered in Jersey.

(*b*) Fresh water

Brown, J. M. (1947). 'Entomology around Robin Hood's Bay.' Naturalist: 108–10.

An account of the distribution of aquatic Hemiptera in seven different kinds of habitat.

Fisher, W. D. (1950). 'Mollusca of a sewage works.' J. Conchol. 23: 113.

An account of the species of Mollusca inhabiting a sewage works at Leeds.

Fox, H. M. (1949). 'On *Apus*: its rediscovery in Britain, nomenclature and habits.' Proc. Zool. Soc. Lond. 119: 693–702.

Apus was recorded in 1738, 1816, 1830, 1907, 1935, 1947 and 1948. The last three records are from the same pool. Haemoglobin in the blood is inversely proportional to the oxygen content of the pool and the animal exhibits a surfacing behaviour when short of oxygen.

Stainforth, T. (1944). 'Reed-beetles of the genus *Donacia* and its allies in Yorkshire (Col. Chrysomelidae).' Naturalist: 81–91, 127–39.

Observations on several species showed clearly the relationship existing between them and certain species of plants.

Taylor, E. W. (1940). 'The freezing of ponds and lakes.' Naturalist: 65.

Where coots and swans were present in numbers they appeared to maintain an area of open water in an otherwise frozen lake, not by continuous movement but by their own animal warmth.

Thorpe, W. H. & Crisp, D. J. (1949). 'Studies on plastron respiration. IV. Plastron respiration in the Coleoptera.' J. Exp. Biol. 26: 219–60.

Studies on the bug *Aphelocheirus* are here extended to a range of water-beetle families. *Haemonia* has a very perfect plastron of stiff hairs bent over at the tips. The Elmidae have less perfect plastra, but can use them to control floating or sinking. The factors in the construction of successful plastra are considered in detail.

(*c*) Land

Beirne, B. P. (1948). 'Notes on the history of the British and Irish bats.' Irish Nat. J. 9: 153–5.

Of twelve indigenous species of bats in Britain, at least seven are considered to be post-glacial invaders, while three date from the Pleistocene Ice Age. Those species whose distribution does not extend into Scotland are also absent from Ireland, while those which occur in Scotland have a widespread distribution in Ireland. This is considered as confirmatory evidence for the existence of a post-glacial land bridge between Islay and N. Ireland as previously deduced (by the same author) from the Lepidoptera. *Myotis nattereri* and *M. mystacinus* are probably Post-Glacial invaders whose present distribution is limited by climatic factors. *Nyctalus leisleri* probably survived the Ice Age in a land mass occupying what is now the Irish Sea. From there it may have spread westwards across the low lying part of Ireland, but its spread eastwards was checked by mountain barriers. The two species of horseshoe bat *Rhinolophus ferrum-equinum* and *R. hipposideros* are represented by endemic subspecies. It is considered that they survived the Ice Age in a land mass to the South of Ireland.

Broadbent, L., Cornford, C. E., Hull, R. & Tinsley, T. W. (1949). 'Overwintering of aphids, especially *Myzus persicae* (Sulzer), in root clamps.' Ann. Appl. Biol. 36: 513–24.

Myzus persicae, *Hyperomyzus staphyleae* and *Aulacorthum solani* in mangold clamps: only *Myzus ascalonicus* was found in swede clamps.

Champness, S. S. (1950). 'Effect of microclimate on the establishment of timothy grass.' Nature, Lond. 165: 325.

Measurements of microclimatic gradients in the top 6–7 in. over bare ground, and in stands of timothy (*Phleum pratense*), white clover (*Trifolium repens*), and timothy plus sow thistle (*Sonchus oleraceus*) showed the protective effect of vegetation, and this is used to explain the failure of timothy seedlings under exposed conditions. These results are also of some interest for the ecology of grassland animals.

Chislett, R. (1940). 'On the birds about a part of the southern county boundary of Yorkshire. A survey of the levels between Hatfield and the Idle, 1929–1939.' Naturalist: 123–32.

A 10-year survey of some 45 square miles of the levels between Hatfield and the river Idle. There are twenty-one different types of habitat, including open moorland, woodland and dykes with varying amounts of vegetation. 104 species have been recorded of which 82 have bred.

Chislett, R. (1945). 'The British willow-tit in Yorkshire.' Naturalist: 127–8.

Queries about the possible relationship of willow-tits with localities where suitable hole-making opportunities are available.

Condry, W. M. (1950). 'The breeding birds of an area of central Wales.' Naturalist: 11–16.

A survey of some 60 square miles mainly in north-east Cardiganshire. The ecological divisions include hill pasture, upland heather tracts, lakes, woodlands and rough agricultural land.

Forsyth, W. G. C. & Webley, D. M. (1949). 'The synthesis of polysaccharides by bacteria isolated from soil.' J. Gen. Microbiol. 3: 395–9.

The numbers of polysaccharide (chiefly gum) producing bacteria varied from 5 to 16% of the total flora in a wide range of soils examined. The polysaccharides are important both as constituents of 'humus' and for their physical effects on the crumb structure of the soil.

Franklin, M. T. (1950). 'Two species of *Aphelenchoides* associated with strawberry bud disease in Britain.' Ann. Appl. Biol. 37: 1–10.

Nematodes, *A. fragariae* and *A. ritzema-bosi*. *A. olesistus* is considered a synonym of *A. fragariae*.

Fraser, F. C. & King, J. C. (1950). 'Preliminary report on the bone remains from Star Carr, Seamer.' Proc. Prehist. Soc. for 1949: 67–9.

Examination of bones from this Yorkshire Mesolithic site shows the presence of red deer (numerous, many of the antlers worked), roe deer (less abundant), elk (least common of the three, but important as providing substantial evidence of the occurrence of the species in England in Mesolithic times), bovid (undetermined), pig, badger, marten, fox, beaver and birds.

Hawson, F. (1947). 'Heather moor ecology, No. 3.' Naturalist: 149–50.

Lepidoptera reports from St Ives, Bingley, for 1944–7.

Hincks, W. D. (1946). 'A preliminary list of Yorkshire Trypetid flies (Diptera, Trypetidae).' Naturalist: 101–7.

This family has been to a great extent neglected in Yorkshire.

Jacob, F. H. (1949). 'A study of *Aphis sambuci* L. (Hemiptera: Aphididae) and a discussion of its bearing upon the study of the "Black Aphids"—Part II.' Proc. R. Ent. Soc. Lond. A, 24: 99–110.

Biology, experimental transference to various host plants, morphological variations in samples from different host plants, at different seasons and possibly geographic variations.

Marriner, T. F. (1940). 'Birds, mammals and fishes of Easton area of N.E. Cumberland.' Naturalist: 177–84.

A study of an inaccessible and little-known area. Special attention is paid to the effect on the wild life of recent changes in agriculture, road surfaces and methods of transport.

Ryves, B. H. (1944). 'Birds and gardens.' Ann. Rep. Cornwall Bird-Watching and Pres. Soc. 14: 71–4.

Notes on the good and harm done by birds to garden trees and plants, based on nearly 25 years' experience.

Smith, A. M. (1945). 'Ecology of heather moor.' Naturalist: 45–8.

An investigation carried out by the Bradford Naturalists at St Ives, Bingley. Soil analyses were made and the plants, insects and birds studied.

Smith, A. M. (1947). 'Heather moor ecology, No. 2. Further report of the survey made by the Bradford Naturalists' Society at St. Ives, Bingley.' Naturalist: 141–9.

Continuation of the investigation at St Ives, largely concerned with soil analysis.

Stevens, C. J. (1948). 'Some observations on roosting in Cornish birds. Ann. Rep. Cornwall Bird-Watching and Pres. Soc. 18: 46–59.

An account of the roosting habits and behaviour of some thirty species.

Stratton, L. W. (1950). 'Habitat of *Clausilia rolphii* Turton.' J. Conchol. 23: 101.

Description of the habitat of a local species of snail recently discovered in Bedfordshire.

Stroyan, H. L. G. (1950). 'A new British aphid species from *Linaria*.' Proc. R. Ent. Soc. Lond. B, 19: 60–3.

Includes notes on biology.

Vowles, D. M. (1950). 'Sensitivity of ants to polarized light.' Nature, Lond. 165: 282–3.

Experiments indicated that *Myrmica laevinodis* and *ruginodis*, like honey-bees, respond to the plane of polarization of light, and orientate themselves in relation to it.

(*d*) Small islands

Brown, D. G. & Sankey, J. H. P. (1950). 'The harvest-spider *Nelima silvatica* (Simon) in Great Britain.' Proc. Zool. Soc. Lond. 119: 867–71.

A consideration of the structure of this species in relation to the same and closely related species from the continent and Britain is followed by notes on its distribution on Skokholm, where it is considered to be the dominant harvestman, and in thirteen other British localities.

Kennedy, P. G. (1947). 'Additional notes on the bird life of the North Bull.' Irish Nat. J. 9: 1–9.

Notes on birds recorded on a small estuarine island in Dublin Bay. Changes in status of certain species since 1936.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Brian, M. V. & Brian, A. D. (1949). 'Observations on the taxonomy of the ants *Myrmica rubra* L. and *M. laevinodis* Nylander (Hymenoptera: Formicidae).' Trans. R. Ent. Soc. Lond. 100: 393–409.

A biometrical study showing that colonies of one species can be distinguished from colonies of the other. As a result Forel's intermediate category *M. laevinodis* var. *ruginodo-laevinodis* will probably disappear. *M. rubra* is shown to exist in two varieties which are both widespread and occur together in some localities: each variety differs primarily in its propagation methods.

Clark, G. (1948). 'Fowling in prehistoric Europe.' Antiquity, 22: 116–130.

An illustrated discussion of the snares, traps and other methods used by prehistoric man for catching and killing many species of birds, including the great auk, grouse, ptarmigan, capercaillie, heron, golden eagle, and various species of ducks, gulls, grebes, etc. Many of these birds were used for food, some may have been killed for their oil or as 'vermin', the eagle provided feathers for fletching arrows, etc. The prehistoric methods of fowling are compared with similar methods still in use among primitive tribes to-day.

Hickin, N. E. (1949). 'Pupae of the British Trichoptera.' Trans. R. Ent. Soc. Lond. 100: 275–89.

Well illustrated and includes a key to the families based on the pupal skin.

Macdonald, W. W. (1950). 'The larvae of *Mystacides azurea* L., *Cyrnus flavidus* McLachlan and *Oxyethira simplex* Ris (Trichoptera).' Proc. R. Ent. Soc. Lond. A, 25: 19–28.

Terminology used in descriptions, method used for rearing larvae and descriptions.

Sankey, J. H. P. (1949). 'On the harvestman, *Opilio saxatilis* (C. L. Koch).' Proc. Zool. Soc. Lond. 119: 297–300.

Morphological and ecological evidence is presented for considering this species to be distinct from *O. parietinus* and a list of known records is included.

Satchell, G. H. (1950). 'The early stages of the British species of *Pericoma* Walker (Diptera: Psychodidae).' Trans. R. Ent. Soc. Lond. 100: 411–47.

Contains keys to larvae and pupae of twelve species. Well illustrated.

3. PARASITES

Cumber, R. A. (1949). 'Humble-bee parasites and commensals found within a thirty mile radius of London.' Proc. R. Ent. Soc. Lond. A, 24: 119–27.

The nematode *Sphaerularia bombi*, an undescribed Tarsonemid mite; Conopidae, *Brachycoma devia* (Tachinidae), *Volucella bombylans* (Syrphidae), *Fannia* spp. (Muscidae) (Diptera); *Aphomia sociella* (Galleriidae) (Lepidoptera); *Epuraea depressa*, *Antherophagus nigricornis*, *Cryptophagus setulosus*, *Leptinus testaceus*, *Ptomophagus varicornis* and *P. subvillosus* (Coleoptera) and *Psithyrus* the parasitic humble-bee.

Evans, G. O. (1950). 'Studies on the bionomics of the sheep ked, *Melophagus ovinus*, L., in West Wales.' Bull. Ent. Res. 40: 459–78.

The life cycle is completed in 33–36 days, the female matures in 6–7 days and the male in 10–11. Copulation takes place 16 hr. after emergence and the first pupa is deposited about 13 days after emergence. Successive pupae are deposited at intervals of 7–8 days. Pupal stage lasts 20–26 days.

The position of attachment of the pupae is controlled by the depth of the fleece, the deposition occurring on the wool fibres where the temperature is suitable. Degree of infestation is influenced by the transference of keds between the sheep.

Hincks, W. D. (1944). 'On the "shirt-button" cocoon of *Dyscritulus planiceps* (Marshall) (Hym. Aphidiidae).' Naturalist: 93–6.

Description and diagram of the cocoon of one of the internal parasites of aphids.

Hopkins, G. H. E. (1949). 'The host associations of the lice of Mammals.' Proc. Zool. Soc. Lond. 119: 387–604.

The greater part of this comprehensive work includes a complete list of known mammal lice and their hosts, the first to be published since 1880. This concerns only about one-fifth of the known mammals. The author's interest is chiefly centred on the evidence for relationship between the mammal species to be derived from a study of their lice. The group provides much evidence of this nature owing to the extreme specificity of the parasites and the fact that the entire life history is usually passed on a single host. Ecological notes include estimations of the numbers of parasites on a single host, the interactions of host and parasite, movements between hosts and records of more than one species on a single host. In the latter respect the Mallophaga of mammals differ conspicuously from those of birds, which commonly have several species confined to certain areas of the body. There is a tendency in mammal-lice for different parts of the life cycle to be limited to certain areas. The work concludes with a bibliography of over 600 works and a table of mammalian synonyms.

O'Mahony, E. (1947). 'The mammal ectoparasites of the North Bull Island, Dublin Bay.' Irish Nat. J. 9: 78–9.

Notes on the mammal ectoparasites of an estuarine island. With the exception of the rabbit louse (*Haemodipsus ventricosus*) all are common species. Although not mentioned by the author, the island has a bridge connecting it to the mainland; and at low tide large mammals can reach it across the mud.

Whitehead, H. (1945). 'Notes on the biology of *Agriotypus armatus* (Walk.).' Naturalist: 123–6.

Brief notes about the one species of this hymenopterous parasite genus found in Britain.

Winter, A. E. (1947). 'Observations on *Dyscritulus planiceps* (Marshall) (Hym. Aphidiidae).' Naturalist: 93–4.

Describes the method by which the parasite larva forms the cocoon and includes photographs of cocoons.

4. FOOD AND FOOD HABITS

Ellis, J. C. S. (1947). 'The rôle of birds in checking defoliating moths.' Naturalist: 52–5.

An account of the extent to which different species of birds fed on the eggs, larvae and moths of *Tortrix viridana* and *Hybernia defoliara* in the sessile oakwoods of the Upper Dearne Valley, Yorkshire.

Thompson, J. L. Cloudsley- (1947). 'The edibility of Hydracarina.' Naturalist: 116–18.

Experiments were carried out on *Hydrarachna schneideri* and *Limnesia maculata*. A summary is given of the extent to which the Hydracarina are eaten in nature.

5. POPULATION STUDIES

Brown, R. H. (1942). 'The autumn and winter habits of rooks and jackdaws.' Naturalist: 39–45.

Eleven years' observations of the winter roost of three rookeries near Carlisle. These include the effect of weather conditions on the timing of morning and evening flocks and notes on behaviour.

Coombs, C. J. F. (1946). 'Roosting of ravens.' Ann. Rep. Cornwall Bird-Watching and Pres. Soc. 16: 49–50.

An account of a roost of 100–150 *Corvus corax* near a comparatively built-up area where an abnormally liberal food supply was available.

Davies, J. L. (1949). 'Observations on the grey seal (*Halichoerus grypus*) at Ramsey Island, Pembrokeshire.' Proc. Zool. Soc. Lond. 9: 673–92.

Behaviour of adults and calves is recorded; calving rate, sex ratio, infant mortality and other vital statistics are presented in a study of population dynamics and movements and are compared with those from Scottish seal colonies.

Hodgson, W. C. & Richardson, I. D. (1949). 'The experiments on the Cornish pilchard fishery in 1947–8.' Fish. Invest., Ser. II, 17, (2): 1–21.

An unusually readable preliminary account of first experiments to find out whether the Scottish ring-net practice can be successfully applied to improve the yield of the Cornish pilchard fishery which at present uses drift-nets. Existing economics of the fishery have been well considered in designing the experimental programme, and early findings show much in favour of the ring-net when used with echo-sounding. The latter is essential: without it ring-netting would be no more profitable than drifting. Standard data on age, maturity, etc. are being collected as well as most interesting facts about the behaviour of pilchard shoals in relation to light, wind, tide, etc., and on the size, distribution density, etc. of shoals. Photographs of echo-traces illustrate this.

Stelfox, A. W. (1948). 'Increase in recent years of the dragonfly *Aeshna grandis* in the Dublin district.' Irish Nat. J. 9: 130.

Since 1920 *A. grandis* appears to have gradually replaced *A. juncea*. No reason for this replacement has been suggested.

Williamson, K. & Cowin, W. S. (1940). 'The rook in the Isle of Man.' Naturalist: 271–82.

A study of the density and distribution of the rook population of the Isle of Man. Results of the censuses of rookeries made in the springs of 1938 and 1940 are included, together with a distribution map. Further notes, on 1941 survey, in (1942) Naturalist: 117–21.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Behura, B. K. (1950). 'A little-known tyroglyphoid mite, *Histiosoma polypori* (Oud.), and its association with the earwig, *Forficula auricularia* Linn.' Nature, Lond. 165: 1025–6.

One of several allied mites known to occur in the British Isles. This species was found in the hypopus stage attached to earwigs in Edinburgh, apparently as a means of dispersal.

Chislett, R. (1940). 'Notes from Spurn, 1939.' Naturalist: 117.

An account both of breeding species and of spring and autumn migratory movements. Comparison is made with the status of migrants thirty years before.

Comfort, A. (1950). '*Hygromia cinctella* (Draparnaud) in England.' J. Conchol. 23: 99.

A species of snail new to British fauna, probably introduced, now well established at Paignton, S. Devon.

Cooper, B. A. (1944). 'Observations on migrating cabbage whites in 1943.' Naturalist: 46–8.

Counts of *Pieris rapae* and *P. brassicae* made in Yorkshire during July and August 1943. The direction of migration is closely related to wind direction.

Dunn, E. (1949). 'Colorado beetle in the Channel Islands, 1947 and 1948.' Ann. Appl. Biol. 36: 525–34.

The beetles can survive up to 10 days in sea water and still be capable of flying when the temperature reaches 80° F. They travelled across about 30 miles of sea to invade Guernsey.

Galbraith, M. & Taylor, M. (1950). 'Dispersal of *Amoeba proteus*.' Nature, Lond. 165: 938.

Experiments proving that *Amoeba proteus* in the young encysted stage can survive drying up, and thus might be dispersed by wind.

Hartley, P. H. T. (1945). 'Sea-bird movements.' Ann. Rep. Cornwall Bird-Watching and Pres. Soc. 15: 72–9.

Summarizes published and unpublished observations on the flight-lines of *Puffinus puffinus* and *Sula bassana* and other sea-birds off the coasts of Cornwall and concludes that in the breeding season the movements are connected directly with feeding and that in the winter, when the birds are no longer bound to their breeding places, they are still affected by the 'tradition' of summer and move by habit along the same routes.

Johnson, C. G. (1950). 'A suction trap for small airborne insects which automatically segregates the catch into successive hourly samples.' Ann. Appl. Biol. 37: 80–91.

The design and operation of a suction trap which takes in air at a constant rate in winds up to 12 m.p.h. The catch is deposited in a collecting tube into which closely fitting discs fall, one every hour, thus segregating the catch into successive hourly samples. The trap is electrically driven: it operates in all weathers and heavy rain does not disorganize the catch.

Johnson, C. G. & Southwood, T. R. E. (1949). 'Seasonal records in 1947 and 1948 of flying Hemiptera-Heteroptera particularly *Lygus pratensis* L., caught in nets 50 ft. to 3,000 ft. above the ground.' Proc. R. Ent. Soc. Lond. A, 24: 128–30.

Of 35,447 insects caught from 23 June to 31 October 1947, 21,334 were aphids and only 37 Heteroptera belonging to the genera *Piesma*, *Nabis*, *Acompocoris*, *Xylocoris*, *Orius*, *Anthocoris*, *Lygus* and *Liocoris*. One out of the twenty-one *Lygus pratensis* was captured at 3000 ft. Most of the Heteroptera appeared in the nets at 50 and 250 ft. In 1948 only 5 Heteroptera were captured although 12,000 aphids were caught.

Kennedy, J. S. (1950). 'Aphid migration and the spread of plant viruses.' Nature, Lond. 165: 1024–5.

The peach-potato aphid *Myzus persicae* can only distinguish its host-plant at a very short distance, mostly after alighting on it. This species would alight on spindle, and then leave again. The migration is partly an active one, not just a passive drift.

Longfield, C. (1948). 'A vast immigration of dragonflies into the South coast of Co. Cork.' Irish Nat. J. 9: 133–41.

Very large numbers of *Sympetrum striolatum* invaded southern Ireland, chiefly Co. Cork, in September 1947. Very few penetrated inland, the mountain barrier checking their progress. A few reached Co. Kildare probably by way of the valley of the Slaney. All the insects appear to have been adults; some were in coition when they arrived from the sea. They all appear to have been *S. striolatum* and an intermediate race of it, nearest to the Atlantic coast subspecies *nigrifemur*. Hence their place of origin was most probably Spain or Portugal. The insects usually arrived on hot sunny days with little wind and kept a N. or N.E. course.

Ruttledge, R. F. (1946–1950). 'Report on observations of birds at Irish Light-Stations, 1945.' Irish Nat. J. 8: 382–7: [1946] 9: 57–61: [1947] 9: 142–5; [1948] 9: 256–60; [1949] 10: 51–5.

Reports on the birds killed or seen at Irish Lighthouses while on migration. Chiefly deal with more exceptional occurrences, but observation is made on 'rushes' of migrant birds. Present reports deal with years 1945–9.

Ryves, B. H. (1947). 'Effects on birds of the severe winter of 1947.' Ann. Rep. Cornwall Bird-Watching and Press. Soc. 17: 5–8.

Summarizes the effect of the severe weather from 22 January to 10 March 1947, on the bird-life of Cornwall under the headings of: mortality, abnormal movements, large-scale migration to Scilly, unusual tameness and behaviour and lowered vitality among birds which survived.

Sullivan, D. J. (1946). 'Remarkable migration of butterflies at night and during a gale in Co. Donegal.' Irish Nat. J. 8: 337.

An account of night migration of *Vanessa atalanta* and *V. cardui* during rain and wind of force 7, at Arranmore Lighthouse on 10 October 1945.

Wigglesworth, V. B. (1949). 'The utilization of reserve substances in *Drosophila* during flight.' J. Exp. Biol. 26: 150–63.

Glycogen is the chief reserve material which may be stored in many parts of the body and disappears during starvation. Exhausted flies can be restored to flight by the administration of glucose and 1 μg. will maintain *D. melanogaster* in flight for an average time of 6·3 min.

7. REPORTS OF ORGANIZATIONS

Annual Report of the Edward Grey Institute [1950]. Ann. Rep. Brit. Trust Orn. for 1949, 16: 20–4.

During 1949–50 the Institute has continued research into the behaviour, breeding biology and population dynamics of various species of titmice (*Parus*), and the breeding biology of the swift (*Apus apus*).

British Trust for Ornithology [1950]. Sixteenth Annual Report, 1949. 48 pp.

Contains reports on the following Inquires for the year: Sample Census of Heronries, Nest Record Scheme, Great Crested Grebe Sample Census, Black Redstart Inquiry, Migrant Swift Watch, Inland Migration of Waders and Terns, Bridled Guillemot Inquiry, Fulmar Investigation, Hobby Survey, Lesser Black-backed Gull Inquiry, Paper-tearing by Birds, Nesting of Titmice; also the annual reports of the Edward Grey Institute for Field Ornithology, and of the Trust's own Bird-ringing Committee, Bird Observatories Committee and Study Material Service. A valuable feature is a list of names and addresses of national and regional organizations concerned with ornithology, local natural history societies, and bodies concerned with international nature protection.

Oundle School Natural History Society [1949]. Annual Report for the 1948 Season. 31 pp.

Work continues to be mainly on faunistic and phenological lines, but a brief survey, which it is hoped to continue, was made of some gravel-pits dug in 1942–3.

Oundle School Natural History Society [1950]. Annual Report for the 1949 Season. 25 pp.

Reporting again mostly faunistic and phenological observations, but with some brief notes on the habitats of Opiliones.

Rugby School Natural History Society (1950). Report for the year 1949. 48 pp.

The 83rd issue of this report contains the results of a waterfowl census throughout the year at Stanford Reservoir, Leicestershire; a check-list of the mammals, reptiles and amphibians of the Rugby district; and a brief account of a survey of the distribution of the mussel *Anodonta* in the district.

West Wales Field Society (1950), Annual Report of, for year ending 31st March, 1950.

Contains papers on 'The kite in Wales To-day', 'The Orielton Decoy', 'Bird protection in Pembrokeshire in 1949' (with a census of the species on St Margaret's Island), 'Birds of the St David's area', and additions and corrections to 'The birds of Pembrokeshire', published by the Society in 1949.

BRITISH ECOLOGICAL SOCIETY

MEETING AT UNIVERSITY COLLEGE, LONDON

Saturday, 22 October 1949

A meeting of the Society was held on 22 October 1949, in the Department of Botany of University College, London, by kind permission of Prof. W. H. Pearsall. The President, Mr C. Elton, took the Chair at 11 a.m. and Prof. A. R. Clapham made a brief introductory statement pointing out that the chief aim of the Meeting was to focus attention on an important activity of the Society, the publication of the Biological Flora of the British Isles. The speakers would assist other contributors by indicating the kinds of problems encountered and the ways in which they could be tackled; and would themselves benefit from the discussions. But the Biological Flora was not be be regarded merely as an end in itself; it was intended that the accounts should be valuable sources of information for workers in many fields of biological research, and members would no doubt hear much of great interest and importance to themselves as ecologists. The programme had been arranged to cover as wide a range as possible. *Juncus squarrosus* and *Calluna* were common and widespread plants of considerable ecological significance, *Lloydia serotina* was an exceedingly rare plant and *Epilobium pedunculare* an established alien, while the aquatic Veronicas presented some taxonomic problems.

The first contributor was Prof. W. H. Pearsall, who spoke on *Juncus squarrosus*. He stated that this species was specially prominent in areas which had been subjected to human interference. His interest had first been aroused by its abundance on Tan Hill, between Swaledale and Upper Wharfedale, and there it marked areas formerly dug for surface coal, where it had persisted for the 150 years which had elapsed since digging had ceased. It was a characteristic plant of heather moors suffering from over-burning and, with *Nardus stricta*, of *Festuca-Agrostis* pastures over-grazed by sheep. It grew usually on 'mor' peat less than 2 ft. thick and of pH 3·5–3·8, and sometimes on extremely leached mineral soil, but was only an occasional plant of deep bog peats. Its substrata were usually saturated with water during the winter but were oxidizing in summer. The chief associates of *Juncus squarrosus* were *Nardus stricta*, *Eriophorum vaginatum* and *Polytrichum commune*, all species with very low nutrient requirements and all indicators of anthropogenic influences which had reduced the nutrient level of the soil.

Germination tests showed an average viability of about 50%, but percentage germination varied strikingly with the substratum and with pre-treatment. Maximal germination (90–100%) was obtained in raised-bog sphagnum peat of pH 3·97, with or without pre-treatment by freezing. On *Eriophorum vaginatum* peat of pH 3·28 germination was poor (5–10%) without, but quite high (30%) with, previous freezing. On fen peat of pH 6·56 germination fell to about 25%, and on peat of pH 7·60, over marl, there was no germination at all.

Juncus squarrosus grew in every vice-county and at all altitudes from sea-level to 3500 ft. There was a reduction in stem length, number of flowers and number of seeds with increasing altitude. Thus average stem length fell from 32 cm. at 700 ft. to 17–18 cm. at 3000 ft.; and ripe seeds were usually not found at altitudes above 2700 ft. though some were collected at 3400 ft. in 1947. In one and the same year 80% germination was obtained from plants growing in *Festuca-Agrostis* grassland and none from plants on *Eriophorum* peat.

No fungi attacked *Juncus squarrosus*, but white larval cases of a small moth, *Coleophora* sp., might be seen on inflorescences of plants growing at altitudes below about 1600 ft.

In the lively discussion following the paper, P. W. Richards, A. R. Clapham, H. Godwin, A. J. Wilmott, C. Elton, A. S. Watt, N. Woodhead, C. Gimingham and Miss S. Champness took part.

Mr C. Gimingham next gave his account of *Calluna vulgaris*, a plant of considerable taxonomic and phytogeographical interest as the only species of its genus, and ecologically important as a dominant of the Atlantic heaths. It was of interest, too, as an hygrophilous mesophyte with xeromorphic characters, and it had great agricultural and aesthetic value. Although it extended from the arctic circle in Iceland and north Scandinavia to Morocco and the Azores, and from the Atlantic seaboard to just beyond the Urals, it was ecologically important only in a restricted area in north-west Europe where it found its

characteristic climatic requirements, a high atmospheric humidity with no period of drought and an absence of prolonged low temperatures. In this country young plants on well-drained soils had suffered from the drought of 1949, and there had been many records of frost damage. Dr A. S. Watt had concluded that it could not survive in mountain areas where snow lay for long periods. Its chief habitats in the country were lowland and upland heaths and moors, bogs, woods with a light or interrupted canopy and sand dunes. The soil was always poor in lime and other bases and acid in reaction. *Calluna* would tolerate a light intensity about 50 % of full daylight but not one of 30 %. It was calcifuge and most plants had a systemic mycorrhizal infection. It grew badly in calcareous soils or in acid soils supplied with calcareous water, and its usual pH range was 3·4–5·9, with an optimum at *c.* pH 4·4. Its rate of transpiration per unit weight was about average, but it seemed to have some capacity of controlling its rate of water loss.

One of the most striking features of *Calluna* was its remarkable plasticity in growth form. It was typically a compact hemispherical shrub, but it developed a long slender 'trunk' and a small crown when in dense stands, and became open and straggly or more or less prostrate at high altitudes. Grazing by sheep or rabbits and burning might lead to a bushy or prostrate form. Experimental treatment of young plants by cutting shoots back with scissors had led to the spreading habit and regular pinnate arrangement of tertiary branchlets found in many burnt or grazed areas. A more intensive grazing or clipping caused the production of numerous short ascending branches so that plants ultimately acquired a small button-like form. The effect of shade was the production of weak stems with long loose branches so that the plants fell open at the centre and allowed lichens and mosses to establish themselves there. *Calluna* communities might die out over large areas if they became even-aged as the result, for example, of simultaneous establishment after fire and so became uniformly susceptible to specially unfavourable climatic effects. The seeds did not seem to require light but their germination occurred sporadically over prolonged periods, up to 3 years from the date of sowing. Dr Poel had found germination at acidities ranging from pH 3 to 10, with optima at pH 4 and 8.

In the discussion, Dr Watt stated that there seemed a considerable genotypic variability in the *Calluna* of Breckland, affecting the hairiness, the colour of leaves and flowers and the direction of growth of lateral shoots. This seemed to contrast with the limited genotypic variability reported from north Scotland. In reply to Mr A. J. Wilmott, Mr Gimingham agreed that adult plants can send functional roots down into limestone or chalk and thought that the calcifuge habit arose from the restricted tolerance of seedlings. C. Elton and J. L. Harley also took part in an interesting discussion.

Mr J. H. Burnett opened the afternoon session with his talk on *Veronica beccabunga*, *V. anagallis-aquatica* and *V. aquatica* (whose correct name would probably turn out to be *V. catenata* Pennell). *V. beccabunga* was easily distinguishable from the other two by its broad petiolate leaves. *V. anagallis-aquatica* and *V. aquatica* had been confused in the past and were certainly much alike, but they could be separated by several characters. Most obviously the flowers of *anagallis-aquatica* were usually pale blue and those of *aquatica* were pinkish. Other useful characters were the ascending pedicels, magenta anthers and capsules narrowed below in *anagallis-aquatica*, contrasting with the horizontally spreading pedicels, reddish anthers and capsules not narrowed below in *aquatica*. Moreover, *anagallis-aquatica* differed in its broader leaves, denser inflorescences with more numerous and larger flowers, and its shorter and narrower bracts. An interesting biological distinction consisted in the frequent infestation of the ovaries of *anagallis-aquatica* and of its sterile hybrid with *aquatica*, but never of *aquatica* itself, by the gall-forming weevil *Gymnometron villosulum*.

Veronica beccabunga, the commonest of the species, had been recorded from every vice-county, while the other two species had a more patchy distribution as judged by information so far obtained, with *anagallis-aquatica* appearing to reach farther north (to the Shetlands). But it seemed likely that fuller data would show that all three, with the hybrid, occurred in every vice-county.

All were plants of open marshy base-rich habitats, especially by streams on the broken trampled soil between reed swamp and the closed turf of meadow or pasture. *V. beccabunga* was distinctly more shade-tolerant than the other two. All set a good deal of seed but seedlings had been observed only on a single occasion and it seemed that reproduction was almost entirely vegetative. *V. beccabunga* would root readily even from internodal fragments no more than 1 cm. in length, and its greater abundance might be relatable to this capacity which was not shared by the other two. All, however, put out short leafy

lateral shoots from the base of the stem in early autumn, and these units became detached during the winter to form new plants in the following season. All, too, could flourish when submerged in fast-flowing water more than 50 cm. deep, the leaves then being broad and thin and only the inflorescences being emergent. In the discussion which followed Dr R. W. Butcher said that he had seen healthy rosettes in much shallower water in some Hampshire rivers. C. Elton, A. J. Wilmott and W. B. Turrill also contributed.

Miss A. J. Davey followed with an account of *Epilobium pedunculare* as a British plant. This native of New Zealand was first observed in the British Isles in 1911, when it was discovered near Ardrishaig in the Clyde valley. At first named *E. nummularifolium*, it was now clear that all naturalized plants so far collected belonged to the different species usually called *E. pedunculare*, characterized by having a glabrous, not cinerascent-pubescent, capsule. It was a small creeping perennial, rooting at the nodes. It favoured moist well-drained and often stony substrata, especially by streams and waterfalls and commonly at considerable altitudes (to 1500 ft.). Its flowers were axillary, with long slender erect peduncles. They were self-pollinated and set copious seed almost all of which germinated if sown immediately but not, apparently, if kept. The remarkable feature of the species was its rapid spread in recent years. For 20 years after its first appearance it remained a rare casual in and near the Clyde district, but from 1930 it extended in range and quantity so greatly as to become a locally abundant plant. It was now known from Raasay southwards to Cornwall and had been recorded also from near Aberdeen, Newcastle-upon-Tyne, Buxton and Tunbridge Wells, and from four Irish counties, Antrim, Tyrone, Fermanagh and Donegal. There were scarcely any records from the eastern side of the country, and it was said to be unable to maintain itself in the neighbourhood of Newcastle-upon-Tyne. It seemed susceptible to drought and its preference for subalpine and western coastal districts might be related to this. A point of interest was its tolerance of such unpromising habitats as slate waste and china clay. In a long and active discussion it was pointed out that it must have been introduced as a living plant and probably as an alpine species for rock-gardens and walls. The related *E. nummularifolium* was certainly to be seen in gardens.

The last contribution was by Mr N. Woodhead on *Lloydia serotina*, a plant strikingly different from *Epilobium pedunculare* in that it had remained in the same localities for 200 years and had shown no sign of spreading. It was confined to four precipices in the mountains of Carnarvonshire, was extremely rare and was decreasing. It was named by Salisbury in 1822 after Edward Lhwyd, Curator of the Ashmolean Museum towards the end of the seventeenth century, who sent plants for Ray to describe. It was an inconspicuous plant whose small whitish flowers were open only during about a fortnight between mid-June and mid-July. The small bulbs produced three leaves annually, two slender grass-like foliage leaves and an outermost nutritive scale leaf which was apparent only in June, becoming shrivelled in July. The bulbs projected for much of their length beyond the surface of the substratum, and successive bulbs formed an obliquely ascending sympodium bearing six functional roots of the current season and numerous persistent older roots. No insects had ever been seen to visit the flowers nor had any ripe fruit ever been found in this country, and it appeared to maintain itself vegetatively. Occasionally daughter-bulbs were produced in the axils of both foliage leaves, this constituting a means of vegetative multiplication. Its four British localities were all on precipitous north-facing volcanic rocks at 1800–2400 ft. It was here protected against both insolation and the full force of south-westerly storms, but it was rarely covered with snow. It was to be found in 'finger-hold grips' and narrow vertical crevices, either alone or with *Rhacomitrium lanuginosum*, or sometimes with *Festuca ovina*, *Silene acaulis*, *Minuartia verna*, *Sedum rosea*, *Thalictrum alpinum*, *Oxyria digyna*, *Frullania* spp., *Campylopus* sp., etc. A problem of great interest was the history of the species as a British plant. Could it have immigrated since the retreat of the ice, or had it survived through one or more glaciations? Its world distribution was markedly discontinuous in the mountains of central Europe and central Asia, in northern Siberia and in five of the western states of the U.S.A. In an active discussion it emerged that the Swiss habitats of *Lloydia* were commonly on north-facing slopes but by no means always so, and that the bulbs were often buried at least 2 in. below the surface of a black humous soil. It was also pointed out that the associates of *Lloydia* were mostly plants favouring a base-rich substratum, and that the volcanic rock on which it grew was in fact basic.

The Meeting concluded with an expression of the thanks of the Society to the speakers, and to Prof. Pearsall for once again extending to the Society the hospitality of his Department.

BRITISH ECOLOGICAL SOCIETY

ANNUAL GENERAL MEETING IN THE DEPARTMENT OF BOTANY, UNIVERSITY COLLEGE, LEICESTER

5–6 January 1950

Thursday, 5 January

The winter meeting of the Society opened at 8 p.m. on Thursday, 5 January, with a Soirée in the Department of Botany, University College, Leicester, about 60 members and guests being present. Refreshments were served, and many interesting ecological exhibits were on view in the Departments of Botany and Zoology. Members of the Leicester Department of Botany showed herbarium specimens and photographs of plants collected last summer in the Monts Dorés, Central France; plants of various forms of *Poa bulbosa* and *P. alpina* whose cytology is being studied by Prof. Tutin; Miss Roles's excellent drawings for the illustrations to the new Students' Flora, and charts and tables showing the results of Mr F. J. Taylor's investigations on the periodicity of algae in Southland Reservoir. Dr J. Jennings, of the Leicester Department of Geography, exhibited maps and charts of the peat stratigraphy of the broads and fens of the middle Bure valley, Norfolk. These showed clearly the effect of a marine transgression in forming silt levées along the river, the resulting ponding of water in the marginal peat-land causing destruction of the original fen woodland and the initiation of various hydrarch successions. The presence of detritus peat revealed the extent of open water in the initial stages of formation of the broads. Dr Godwin showed a beautiful and instructive set of black and white photographs taken during the Ninth International Phytogeographical Excursion in Eire in July 1949; and Mr A. D. Bradshaw demonstrated a valuable method for studying the growth habit of grasses. At 9 p.m. Dr Godwin projected a series of delightful colour photographs of Irish vegetation, amongst them very successful studies of such interesting components of the flora as *Trichomanes radicans*, *Sisyrinchium angustifolium*, *Eriocaulon septangulare*, *Arbutus unedo*, *Saxifraga spathularis* and the limestone vegetation of County Clare. Members left at about 10.45 p.m. after a very enjoyable gathering.

Friday, 6 January

The Annual General Meeting opened at 10 a.m. with the reading and signing of the minutes of the last annual meeting. The election of sixteen new members was followed by the reading of the Hon. Secretaries' Report in the form already approved by Council:

Report of the Hon. Secretaries for the year 1949

The thirty-fifth Annual Meeting of the Society, attended by about 100 members and guests, was held in the Department of Botany, University College, London, on Friday, 7 January 1949, following a Soirée and an exhibit of ecological work on the previous evening. The business meeting at 11 a.m. was followed by Mr C. S. Elton's interesting and thought-provoking Presidential Address on 'Population Interspersion'. After lunch four ecological papers were read and discussed. The Society has once again to thank Prof. Pearsall and his colleagues for their generous hospitality.

On Saturday, 14 May, Dr Tyge Böcher, of Copenhagen, gave a lecture to the Society in the Department of Botany, University College, London. His subject was 'Distributions of Plants in the Circumpolar Area in Relation to Ecological and Historical Factors'. The members present heard with great interest an account of Dr Böcher's studies of the vegetation of West Greenland and his views on the role of local climatic and edaphic factors in the persistence of plant species during periods no longer favouring their wide distribution.

At the renewed invitation of Prof. Walton the Summer Meeting was held in Glasgow from Tuesday, 2 August, until Saturday, 6 August, members being accommodated in Queen Margaret Hall and its Annexe. The meeting opened with a Soirée in the Department of Zoology, when about 60 members and

guests enjoyed a most pleasant evening. On the following days visits were paid to the Loch Lomond Freshwater Biological Station and Insect Field Station, the Ballochraggan Experimental Area of the West of Scotland Agricultural College, the Marine Biological Station at Millport, Isle of Cumbrae, and the Forestry School and Scottish National Forest Park at Benmore, Argyll. There were also excursions to Flanders Moss and to Ben Narnain, the ascent of which revealed some differences between members taking part. The full and varied programme included also a Reception by the Court of Glasgow University, when the Society was shown the Hunterian Museum and Collection, and a Dinner at Queen Margaret Hall at which the Society entertained the officials of the Andersonian Naturalists' Society. The Society is deeply grateful to Prof. Walton and Prof. Yonge for the hospitality of their Departments, and to Dr E. Conway and Mr Hutchinson of the Glasgow Department of Botany for arranging the programme of this enjoyable meeting.

On Saturday, 22 October there was held in University College, London, a meeting the object of which was to focus attention on an important activity of the Society, the publication of the Biological Flora of the British Isles. After an introductory statement five contributors to the Flora gave interim reports on their work. Prof. Pearsall and Dr C. Gimingham dealt with aspects of the autecology of *Juncus squarrosus* and *Calluna vulgaris* respectively, common and widespread species of considerable ecological significance; Mr J. Burnett described the three aquatic Veronicas, *V. beccabunga*, *V. anagallis-aquatica* and *V. aquatica*, with special reference to the differences between the last two; Miss A. J. Davey gave an interesting account of the history in the British Isles of the alien *Epilobium pedunculare*, and Mr N. Woodhead concluded with an account of that inconspicuous but ecologically glamorous plant *Lloydia serotina*. The meeting emphasized the width and variety of the problems encountered in these autecological studies and it is hoped that members will have been encouraged to undertake further work for the Flora.

During the year the second part of volume 36 and of the first part of volume 37 of the *Journal of Ecology* appeared, while the second part of volume 37 will appear at any moment. The second part of volume 36 contained twelve original papers and three contributions to the Biological Flora, and with reviews and notices totalled 141 pages; while volume 37 contains twenty-two original papers with two contributions to the Biological Flora and various notices and reviews, the total length being 432 pages.

The second part of volume 17 of the *Journal of Animal Ecology*, with sixteen original papers and 276 pages in all, appeared early in the year and the first part of volume 18 in May. This part contained 136 pages in all, with eight original papers, one special review and seven book reviews. The second part of volume 18 will appear shortly.

During the year there were published in the *Journal of Ecology* accounts for the Biological Flora of the genus *Urtica* with *U. dioica* and *U. urens*, the genus *Cuscuta* with *C. europaea*, *Orchis purpurea*, the genus *Eleocharis* with *E. palustris* and *E. uniglumis*, and *Arum maculatum*.

Since the last Annual Meeting the membership of the Society has risen from 595 to 647, 18 members having resigned or died and 70 new members having been elected. Of the present membership 337 take the *Journal of Ecology* alone, 192 the *Journal of Animal Ecology* alone, 109 receive both *Journals* and 9 neither.

The Society records with regret the death of a distinguished member in Mr D. J. Scourfield.

It is with very great pleasure that we note the award in the New Year Honours List of a knighthood to Prof. A. G. Tansley, twice President of this Society, for many years Hon. Editor of the *Journal of Ecology* and now an Hon. Life Member. Prof. Tansley, after a most distinguished scientific career, played an outstanding role in the establishment of the Nature Conservancy, of which he has been appointed the first Chairman.

A. R. Clapham
L. A. Harvey } *Hon. Secretaries*

Arising from this Report, Captain Diver proposed, and it was agreed with acclamation, that a letter of congratulation should be sent to Prof. A. G. Tansley.

The Report of the Hon. Treasurers for the year 1949 was read by Mr V. S. Summerhayes, who said that the financial statement for the year was still incomplete, but that an estimated balance of about £200 might be increased more or less substantially by sales of back numbers of the two *Journals*. Sales of

current *Journals* were increasing satisfactorily, including those of the *Journal of Animal Ecology* which had hitherto been rising very slowly. Although printing costs were to increase by 7½% the financial position of the *Journals* appeared likely to remain satisfactory. Subscriptions brought in about the same amount (*c.* £830) as in 1948, and there was a substantial income, exceeding £130, from investments. Future expenses might include a greater outlay on the Biological Flora and on index volumes for the two *Journals*. It was pleasing to report that sales of the Index to the first twenty volumes of the *Journal of Ecology* had covered the initial outlay and were now providing a steady small profit.

In reply to Prof. P. W. Richards, Dr H. Godwin stated that about one-half of the cost of the contributions to the Biological Flora which appeared in 1948 had been covered by sales in that year; and in reply to Mr G. M. Spooner he said that American sales of the *Journals* might well be increased as the result of the establishment of a New York agency of the Cambridge University Press.

The President, Mr C. S. Elton, then proposed from the Chair that the Society renew its subscriptions to the Freshwater Biological Association, the Biological Council and the British Co-ordinating Committee of Societies for Nature Conservation; and Dr H. Godwin proposed the re-election of the Auditors, Messrs William Norman and Sons, both proposals being carried. A vote of thanks to the Hon. Treasurers was proposed by Prof. T. G. Tutin and approved with acclamation.

The Meeting then proceeded to the election of Officers and Members of Council as follows:

President: W. B. Turrill.

Vice-President: I. Hepburn.

Hon. Secretaries: A. R. Clapham, G. Varley.

Hon. Treasurer: C. E. Hubbard.

Hon. Editors: H. Godwin, C. S. Elton.

Hon. Editors of the Biological Flora: A. R. Clapham, H. Godwin, P. W. Richards.

Ordinary Council Members: D. E. Coombe, J. B. Cragg, J. L. Harley, J. A. Kitching, Miss J. Lambert, E. D. Le Cren, E. W. Russell, D. H. Valentine.

In the absence of the President-elect the retiring President, Mr C. S. Elton, remained in the Chair for the rest of the Meeting.

The Meeting signified its cordial agreement with expressions of the Society's great indebtedness to two retiring Officers, Prof. L. A. Harvey, an Hon. Secretary, and Dr A. S. Watt, an Hon. Treasurer.

In reporting on the *Journal of Ecology* the Hon. Editor, Dr H. Godwin, stated that the second part of volume 37 would appear in the following week and that the first part of volume 38 was complete save only for the account of the Annual Meeting and the List of Members. He appealed for papers not exceeding 15–20 pages in length.

The Hon. Editor of the *Journal of Animal Ecology*, Mr C. S. Elton, said that the next part would appear in February. Papers were being submitted at about the usual rate, but more and more editorial labour was involved in checking the statistical methods employed by authors. The notices of papers in the field of animal ecology appearing elsewhere were now being prepared by Mr Richard Fitter, whose voluntary help was much appreciated. Members were asked to assist Mr Fitter's efforts to make these abstracts as comprehensive as possible.

Prof. P. W. Richards stated that accounts for the Biological Flora of three genera and seven species had been published during 1949, and that four more accounts would appear in the second part of volume 37. Contributors were urged to communicate with the mycological and entomological referees at an early stage and not to leave their requests for expert assistance until their accounts were otherwise complete. They were also advised that the Botanical Society of the British Isles had a panel of referees for critical groups of higher plants, and that these referees would be available for consultation by contributors. It was especially important that specimens of species of which accounts were being written should be deposited either at the British Museum or at Oxford.

Prof. T. G. Tutin acknowledged the receipt, as in previous years, of a parcel of provisions for the Soirée from Miss W. M. Curtis of Hobart, Tasmania, a member of the Society.

In concluding the business meeting the President expressed the Society's deep gratitude to Prof. T. G. Tutin and the authorities of University College, Leicester, for their hospitality on this occasion.

About 60 members and guests were present when, at 11 a.m., Dr A. S. Watt opened the second stage of the meeting with his paper on 'Bracken and frost'. Bracken has spread greatly during the last hundred years or so, both into agricultural land and into areas from which it must be presumed to have been excluded previously by natural causes. Three main biotic factors may be identified as favouring this recent spread: first, the much reduced exploitation of bracken for various industrial purposes and as litter; secondly, the greatly reduced intensity of grazing by cattle; and thirdly, the impaired competitive power of *Calluna* as the result of burning on a short rotation of 10–15 years. But some of the phenomena of spread remain unexplained by these factors, and Dr Watt suggested that a change in climate has been responsible. Since 1850, winter temperatures have risen throughout the north temperate and arctic regions, and more markedly so since 1900. Mean winter temperatures in west and central Europe have averaged about 5° F. higher in the period 1901–30 than in the period 1851–1900. Bracken suffers from frost in two ways. Hard winter frosts may kill fronds and rhizome apices which are close to the surface, and late spring frosts damage or kill fronds which have recently emerged. The hard winters of 1936 and 1947 killed about 30% of the fronds and up to 4% of the rhizome apices in a Breckland area, and that of 1940 killed 79% of the fronds and 44% of the rhizome apices. The winter frosts of 1940 also caused a recession of 5 ft. in a previously advancing bracken front. The susceptibility of apices varies with their depth below the surface and also with the depth of litter on the surface. Fronds near the invading front are more readily killed than those in the hinterland because of the sparse litter, but rhizome apices are on the average nearer to the surface in the hinterland. The effect of litter was demonstrated by removing it from certain quadrats and adding it to others, the former treatment increasing, the latter decreasing, the deaths by frosting as compared with controls. Correlations between total numbers of living emerged fronds and the incidence of frosts are obscured by two other factors: the replacement of killed fronds from the reserve of dormant buds, and the killing of young fronds by desiccation in June droughts. It is, nevertheless, clear that if the warmer winters of this century have been associated with fewer, shorter or less severe spells of frost, they may well have enabled bracken to spread into new areas. C. S. Elton, G. M. Spooner, C. Diver, M. D. Poore, J. D. Ovington and L. W. Poel took part in an active discussion.

Mr L. W. Poel next spoke on 'Soil aeration and the growth of bracken', describing observations made on the Ballochraggan Experimental Area of the West of Scotland Agricultural College. Small patches of bracken in a waterlogged area otherwise devoid of fronds were shown to be associated with large stones, slightly raised ground, remains of old walls or other features affecting drainage and aeration. There was almost invariably a connexion, by living or dead rhizomes, with the surrounding Pteridietum, and it was concluded that the whole area was formerly dominated by bracken which had been suppressed locally by impaired drainage. When streamlets were diverted through bracken-dominated land the fronds became flaccid in 24 hr. and were killed after 2 months, though some healthy rhizomes with living buds could be found even after 2 years. Pot experiments confirmed the sensitivity of bracken to deficient aeration. C. S. Elton, A. S. Watt, C. Diver and J. S. Turner took part in the discussion following this paper.

Miss G. C. Evans then described her work on 'The ecology of *Lepidochitona cinereus* (L.)'. This primitive shore-living mollusc, which feeds on rock-encrusting algae and is very common on suitably pebbly beaches, was studied in Cornwall, at Plymouth and especially at Whitstable where it inhabits the drier part of the *Fucus* zone. This zone is characterized at low tide by considerable areas of very shallow standing water, and *Lepidochitona* shows a preference for these pools and for pebbles about the size of tangerines. At low tide it is almost entirely restricted to the undersides of stones, and if a stone is overturned the displaced individuals begin to move within about 3 min. until they are again on the underside. The resulting movements are therefore downwards, to regions of lower light intensity, higher humidity and greater dorsal contact. Experiments designed to identify the operative factors showed: first, that *Lepidochitona* is not certainly phototactic but moves much more rapidly in bright than in dim light; secondly, that it is positively geotactic when out of water but not when submerged; thirdly, that it does not move along a humidity gradient, though it is very sensitive to water-loss in dry air; and, fourthly, that it makes no regular response to variations in dorsal pressure. The first two types of response would cause individuals to move rapidly downwards when uncovered by the falling tide and to tend to aggregate beneath the stones, but

if stones exceed a certain optimal size death from desiccation may ensue before the edge can be reached. The meeting was adjourned for lunch at this point, and the discussion of Miss Evans's paper, in which G. M. Spooner, C. Diver, H. Godwin and Mrs M. D. Poore took part, was deferred until the resumption at 2.15 p.m.

The first paper of the afternoon session was that by H. P. Moon on 'Certain aspects of the feeding of aquatic insects'. Faecal pellets of Chironomid larvae, cultured under sterile conditions, were shown to contain living algal cells. A starved larva retained some food in its gut for 5 days, and some cells of *Chlamydomonas* and other algae remained alive throughout this period, though *Tribonema* and *Hormidium* survived only for 20 hr. Using mayfly nymphs and pure cultures of various algae it was shown that *Scenedesmus* and *Gonium* often did, but *Sphaerocystis* and *Eudorina* did not, survive passage through the gut. The insects studied pack food into their gut without crushing it, and some cells near the centre of the cylinder are presumed to escape digestion. Further work on this topic is in progress. C. S. Elton, E. Lind, M. B. E. Godward, A. S. Watt, H. Godwin, G. M. Spooner and E. W. Jones took part in a lively discussion.

Miss J. Lambert followed with her paper on 'The vegetation of the broads and fenland of the Bure valley, Norfolk'. The Norfolk Broads originated during a period of marine transgression when silt deposited along the rivers and forming levées caused ponding of water in the marginal peat-land. Since the silt banks widen downstream, the lower broads are farther from the river than are the upper. Miss Lambert dealt chiefly with the less disturbed private broads of the middle Bure valley, from Hoveton Great and Little Broads downstream to Upton Broad. These, except only for Upton Broad, are now connected with the river by artificial cuts and are therefore affected by tidal circulation, this being greatest in the upstream broads which are nearest to the river, very small in the more distant downstream broads and absent in the unconnected Upton Broad. The original limits of open water have been established from the distribution of lake muds as revealed in borings, and Miss Lambert showed from old maps that until about a century ago there had been little diminution in the area of open water, presumably through active maintenance of the banks and exploitation of the marginal vegetation. The hydrarch successions in the various broads were studied by observations both of present zonations and of the succession of dominant species in borings. Three main types were recognized, differing chiefly in the dominants of the sedge-fen stage. All have *Typha angustifolia* as the chief reed-swamp dominant, and all culminate in fen woodlands, though these show considerable differences in structure and floristic composition. The most widespread succession is that in which a *Typha-Phragmites* reed-swamp is succeeded by 'tussock fen' dominated by *Carex paniculata*. Sallows, buckthorns and alders become established on these tussocks and close to form a 'swamp-carr' with persistent *Carex* tussocks and intervening soft peaty pools, often green with *Lemna*. Most of the trees lean owing to the instability of the substratum and there are numbers which have died as the result of the sinking of the surface. In this succession the *Carex* tussocks enable woody plants to colonize before the fen surface is consolidated by rhizomatous species, and this accounts for the treacherous pools and for the failure of the trees to maintain themselves erect. At the other extreme is a succession with *Cladium mariscus* as the dominant of a sedge fen stage which is long-lived and which is succeeded by a *Phragmites* stage. This is entered by woody plants to form a fen woodland containing birch, oak and ash as well as sallow and alder, and having a more or less continuous ground vegetation. In this succession the surface peat is much firmer owing to the well-developed *Cladium* mat, the trees remain erect and the floor of the carr is relatively dry. In an intermediate successional type, of limited occurrence, the sedge is dominated by *Carex acutiformis* and passes into a 'semi-swamp carr' with erect trees. The distribution of these successions suggests that circulating water from the river favours the *C. paniculata* type (very prominent in Hoveton Great Broad) as against the *Cladium* type (the only one in Upton Broad), with the *Carex acutiformis* type intermediate in demands. The immediately operative factors have not yet been identified, but variations in the supply of mineral salts are likely to be more important than the degree of aeration. In Surlingham Broad, in the Yare valley, a much greater tidal circulation is associated with the prevalence of *Glyceria maxima*, but Rockland Broad, farther from the River Yare, has some areas of *Typha-Carex paniculata* fen and appears intermediate between typical Yare and typical Bure broads. Successions on the peats and peaty muds, marginal to the original open water, were also studied. When undisturbed a *Phragmites* reed-swamp is succeeded by 'pseudo-swamp carr' in which the surface mat may suffer local breakdown to give treacherous bare patches, but there is

no open water and the trees remain erect. These communities are commonly exploited and are then deflected to secondary fens such as those dominated by *Juncus subnodulosus* and *Molinia coerula*. H. Godwin, E. Lind and G. M. Spooner took part in the discussion which followed this interesting paper.

The last paper was that by M. Kassas, 'A fen woodland through 160 years', describing a 40-acre conifer plantation on Chippenham Fen, near Newmarket. The trees planted on newly drained peat in 1791 were Scots pine, larch and spruce, but several species of deciduous trees have established themselves since that date. From observations on the survival of the original plantings, the establishment of other woody species and the ground vegetation the area may be divided into three zones arranged more or less symmetrically about a transverse axis. In the central zone, A, farthest from the marginal drains, 54% of the trees are *Fraxinus* less than 50 years old and 22% are *Quercus* less than 100 years old. In the intermediate zone, B, young trees of *Fraxinus* constitute 66·5% and *Acer pseudo-platanus* 20·1%; while in the marginal zone, C, adjoining the drains, *Fraxinus* and *Acer* are about equally abundant and account for almost 93% of all trees. In zone A the ground vegetation is dominated by *Molinia* with some *Phragmites*, in B by *Eupatorium cannabinum* and in C by *Hédera helix*. The zones were found to be delimited by peat-depth contours of 60 cm. (A/B) and 40 cm. (B/C) respectively. Zone A lies over a shallow valley in the original clay floor where water tends to collect, as shown by observations of the height of the water-table in pits dug for the purpose. It appears that *Quercus-Fraxinus-Acer* form a series in respect of tolerance of waterlogging, *Quercus* being most and *Acer* least tolerant. Counts and width measurements of the tree-rings showed consistently a first period, *c.* 1800–50, when rings were wide; a second, *c.* 1851–1915, when they were narrow, and a third, 1915–49, when they were wide except during the years 1932–43. Trees outside the plantation showed a uniform ring-width. Historical records explain these variations in terms of the effectiveness of the drains, 'numerous and deep' as first cut by Tharp in 1791, but become so choked by 1903 that *Selinum carvifolia* was seen that year in 18–24 in. of water. The drains were cleared in 1918 and again in 1942, wider rings following each operation. These great changes in drainage explain also the present distribution of species and age groups in the three zones. Most of the trees originally planted in zone A have died, maximum survival being in zone C. Colonization by self-sown *Betula* and *Fraxinus* started before 1850 and became rapid again after 1918, especially in zone B, where the advantage of improved drainage was not offset (as in C) by the shade cast by surviving old trees. Presumably, for the same reasons, zone B has acquired a shrub layer of *Ligustrum* and *Prunus spinosa*. H. Godwin congratulated the speaker on his presentation of these interesting observations.

A very successful meeting concluded at 5 p.m. with tea in the College refectory.